SHOUT
SHARE
IT

7.1.83

S. BM.1035

GENERAL
1980
LIBRARY
NATURAL HISTORY

Bulletin of the British Museum (Natural History)

Zoology series Vol 37 1979-1980

British Museum (Natural History)
London 1980

Dates of publication of the parts

No 1	29 November 1979
No 2	20 December 1979
No 3	31 January 1980
No 4	28 February 1980

ISSN 007–1498

Printed in Great Britain by Henry Ling Ltd, at the Dorset Press, Dorchester, Dorset

B C NERAL
LIBRARY
NATURAL HI ORY

Contents

Zoology Volume 37

Page

No 1 Miscellanea

Reticulopodia in testate amoebae (Rhizopodea : Protozoa)
Ronald H. Hedley & Colin G. Ogden 1
Review of the genus *Guaranidrilus* (Oligochaeta, Enchytraeidae) with the description of two new species
Brenda Healy 7
Larval development of British prawns and shrimps (Crustacea : Decapoda : Natantia). 3. *Palaemon* (*Palaemon*) *longirostris* H. Milne Edwards, 1837 and the effect of antibiotic on morphogenesis
A. A. Fincham 17
The larval development of the spider crab *Rochinia carpenteri* (Thomson) [Oxyrhyncha : Majidae] with a review of majid subfamilial larval features
R. W. Ingle 47
On the spider genus *Cynapes* (Araneae : Salticidae)
F. R. Wanless 67
A new species of *Phthiracarus* (Acari, Cryptostigmata) from Austria
B. W. Parry 73

No 2 The echinoderms of Aldabra and their habitats
N. A. Sloan, A. M. Clark & J. D. Taylor 81

No 3 The anatomy, phylogeny and classification of bariliine cyprinid fishes
G. J. Howes 129

No 4 The Fellodistomidae (Digenea) of fishes from the northeast Atlantic
R. A. Bray & D. I. Gibson 199

Bulletin of the British Museum (Natural History)

Miscellanea

Zoology series Vol 37 No 1 29 November 1979

The *Bulletin of the British Museum* (*Natural History*), instituted in 1949, is issued in four scientific series, Botany, Entomology, Geology (incorporating Mineralogy) and Zoology, and an Historical series.

Papers in the *Bulletin* are primarily the results of research carried out on the unique and ever-growing collections of the Museum, both by the scientific staff of the Museum and by specialists from elsewhere who make use of the Museum's resources. Many of the papers are works of reference that will remain indispensable for years to come.

Parts are published at irregular intervals as they become ready, each is complete in itself, available separately, and individually priced. Volumes contain about 300 pages and are not necessarily completed within one calendar year. Subscriptions may be placed for one or more series. Subscriptions vary according to the contents of the Volume and are based on a forecast list of titles. As each Volume nears completion, subscribers are informed of the cost of the next Volume and invited to renew their subscriptions. Orders and enquiries should be sent to:

Publications Sales,
British Museum (Natural History),
Cromwell Road,
London SW7 5BD,
England

World List abbreviation: *Bull. Br. Mus. nat. Hist.* (Zool.)

© Trustees of the British Museum (Natural History), 1979

ISSN 0007-1498

Zoology series
Vol 37 No 1 pp 1–79

British Museum (Natural History)
Cromwell Road
London SW7 5BD

Issued 29 November 1979

GENERAL
- [illegible] DEC 1979
LIBRARY
NATURAL HISTORY

Miscellanea

Contents

Page

Reticulopodia in testate amoebae (Rhizopodea : Protozoa). By Ronald H. Hedley & Colin G. Ogden 1

Review of the genus *Guaranidrilus* (Oligochaeta, Enchytraeidae) with the description of two new species. By Brenda Healy 7

Larval development of British prawns and shrimps (Crustacea : Decapoda : Natantia). 3. *Palaemon* (*Palaemon*) *longirostris* H. Milne Edwards, 1837 and the effect of antibiotic on morphogenesis. By A. A. Fincham 17

The larval development of the spider crab *Rochinia carpenteri* (Thomson) [Oxyrhyncha : Majidae] with a review of majid subfamilial larval features. By R. W. Ingle 47

On the spider genus *Cynapes* (Araneae : Salticideae). By F. R. Wanless . . . 67

A new species of *Phthiracarus* (Acari, Cryptostigmata) from Austria. By B. W. Parry 73

Reticulopodia in testate amoebae (Rhizopodea: Protozoa)

Ronald H. Hedley & Colin G. Ogden

British Museum (Natural History), Cromwell Road, London SW7 5BD

Summary

The pseudopodial system of *Cryptodifflugia oviformis* and some other testate amoebae consists of numerous filopodia when examined at the resolution of the optical microscope. These filopods are seen to be part of a full reticulum when examined at the ultrastructural level. It is suggested that the general assumption that testate amoebae produce a filopodial system and foraminifera a reticulopodial system may be invalid.

Introduction

The basic difference between lobopod, filopod and reticulopod pseudopodia as found in the class Rhizopodea, Protozoa, is their shape. Lobopodia are blunt extensions of the cytoplasm such as those found in most of naked amoebae and large testate amoebae; filopodia are usually single tapering cytoplasmic extensions as, for example, in *Euglypha* and other small testate amoebae, whilst reticulopodia are normally the granular anastomosing networks of cytoplasm produced by foraminfera. These basic differences are recognized in standard classifications of the rhizopods (e.g. Honigberg *et al.*, 1964; Loeblich & Tappan, 1961, 1964). Most rhizopods produce pseudopodia which are readily assigned to one of these three basic types. Variants of the three types are well known: for example, Page (1975, 1976) illustrates some naked amoebae which produce filose-like pseudopodia and Leidy (1879) in his account of Freshwater Rhizopoda of North America reports a variety of pseudopodial forms in testate amoebae. There is little confusion between the two extreme forms – lobose and reticulose – but in some protozoa either type may merge into the filose type. Greater confusion exists in certain testate amoebae which possess pseudopodia showing a tendency towards both the lobose and reticulose forms.

This account is concerned with observations at the optical and ultrastructural level of the pseudopodial system in *Cryptodifflugia oviformis*, a cosmopolitan soil and moss inhabiting testacean whose general biology, taxonomy and fine structure have been reported previously by Hedley *et al.* (1977).

Materials and methods

A clonal culture of *Cryptodifflugia oviformis* was isolated from the moss, *Eurhynchium praelongum*, by Hedley *et al.* (1977), and formed the working cultures for this study. It is now deposited at the Culture Centre for Algae and Protozoa, The Natural Environment Research Council, Cambridge, England (Reg. No. 1514/2). Live animals from these cultures were examined by both phase-contrast and bright field illumination. For transmission electron microscopy, specimens were fixed for 12 min. in 1% glutaraldehyde in 0·025 M cacodylic acid buffer, followed by 7 min. in 3% glutaraldehyde in the same buffer. After several rinses in the buffer solution, they were post-fixed with 1% osmium tetroxide in distilled water. The material was dehydrated and embedded in Epon 812. Sections cut with a diamond knife on a Porter Blum ultramicrotome were stained with a saturated solution of alcoholic uranyl acetate and Reynold's lead citrate, and examined in an A.E.I. 6B electron microscope operating at 60 kV. The results were recorded on Ilford EM 6 plates.

Bull. Br. Mus. nat. Hist. (Geol.) **37** (1): 1–6 Issued 29 November 1979

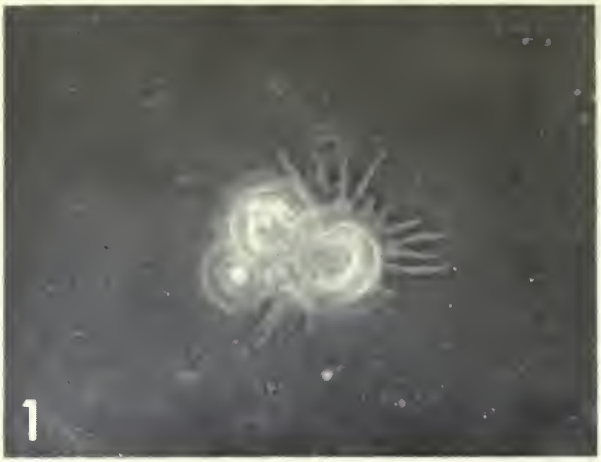


Fig. 1 Phase-contrast micrograph of *Cryptodifflugia oviformis* to show the typical arrangement of filopods, ×520.

Results

The pseudopodial system of actively moving specimens of *Cryptodifflugia oviformis* usually consists of several tapering cytoplasmic extensions which may have small branches, and appear to represent a typical filopodial system (Fig. 1). At the ultrastructural level (Fig. 2) the pseudopodial system is seen to consist of the main filopods and many additional cytoplasmic strands, ranging in diameter from 45 nm to 3 µm, which are reminiscent of those seen in foraminifera. If one identifies in such a micrograph as Fig. 2 those pseudopodia which would normally be seen with the optical microscope, that is those whose diameter is greater than 1 µm (Fig. 3), some explanation is needed for the remainder of the cytoplasmic strands in the micrograph. At a higher magnification (Fig. 4) these connecting cytoplasmic strands are similar to those found in foraminifera with a reticulose network (see Figs. 8 and 9).

A model of the type of pseudopodial arrangement which would be consistent with the micrograph (Figs. 2 and 3) is presented in Figs 5 and 6. This represents only one of many possible arrangements of the pseudopodia which would correspond to such a micrograph. The contraction of the filopods as depicted in Fig. 5 is what one would expect, and does observe when an animal with an extruded filopodial system is immersed and subsequently fixed in glutaraldehyde.

Discussion

In describing the biology and ultrastructure of *Cryptodifflugia oviformis*, Hedley *et al.* (1977) stated that previous studies, among which de Saedeleer (1932) may be mentioned, had drawn attention to the fact that the pseudopodia appeared to be intermediate in form between lobose

---

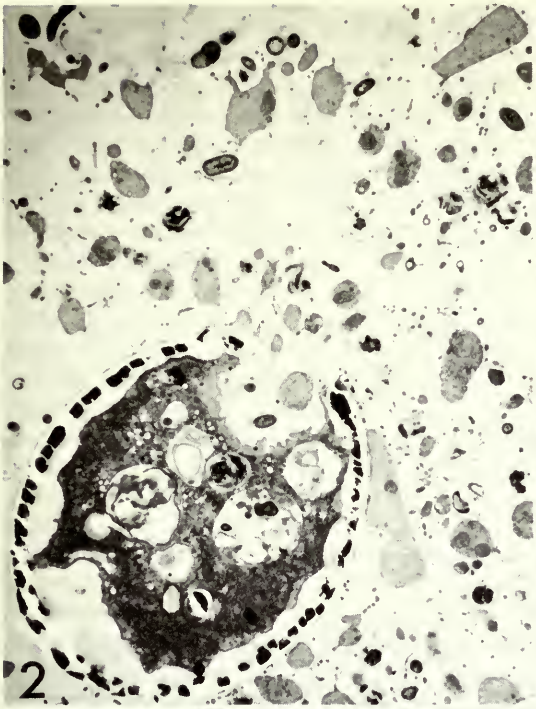
Fig. 2 Section of a specimen of *C. oviformis* to illustrate the range of pseudopodial structures visible at the ultrastructural level, ×4300.

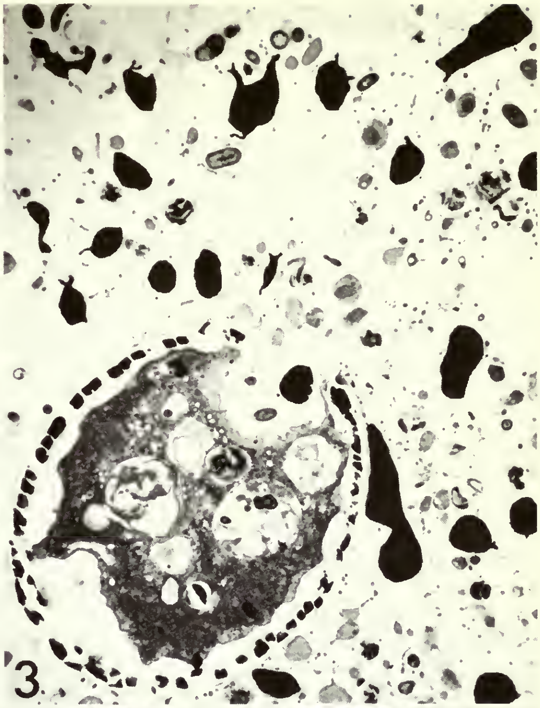
Fig. 3 Section as in Fig. 2 showing those pseudopodia with a diameter greater than 1 µm masked in black, ×4300.

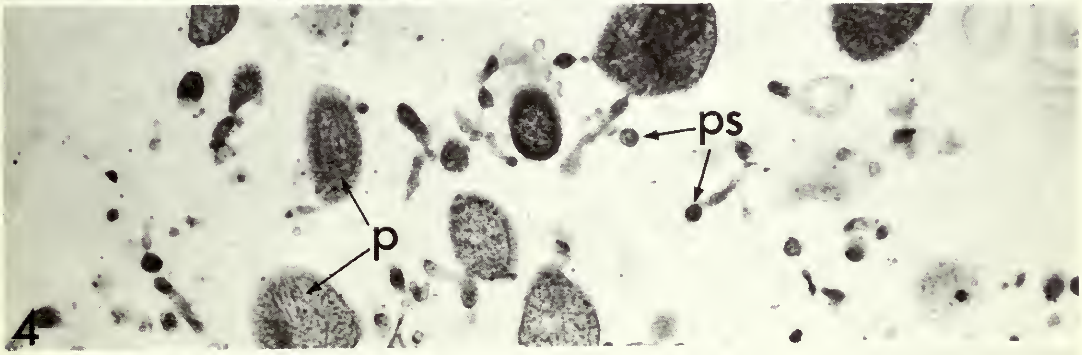
Fig. 4 Section of pseudopodia (p) and pseudopodial strands (ps) near the aperture of *C. oviformis*, ×21 000.

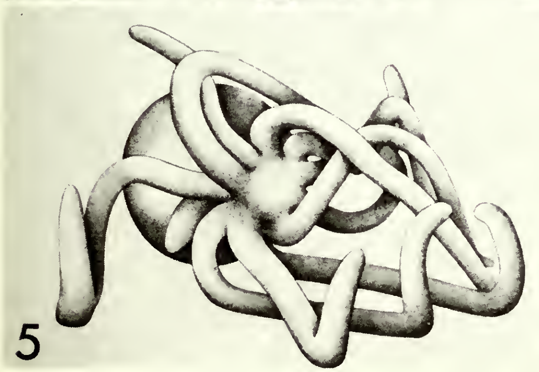
Fig. 5 A model of a specimen of *C. oviformis* to correspond with the micrographs shown in Figs 2 and 3.

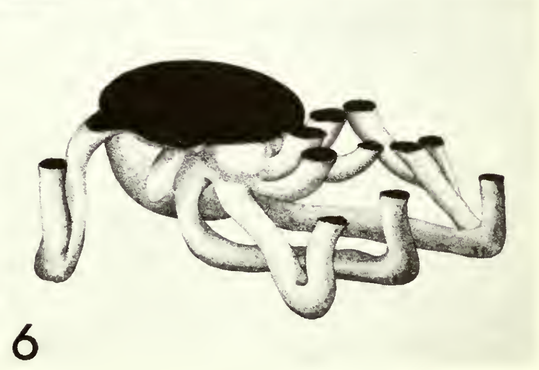
Fig. 6 Diagram to show model cut in the same plane as the sections in Figs 2 and 3.

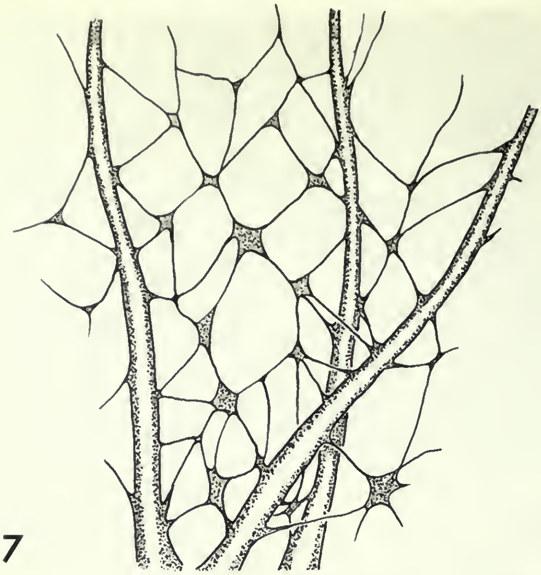

2


3


4

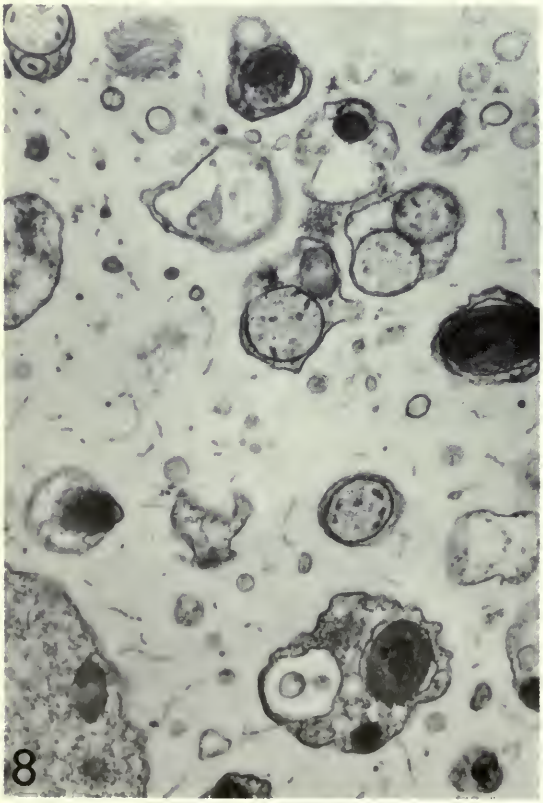

5


6

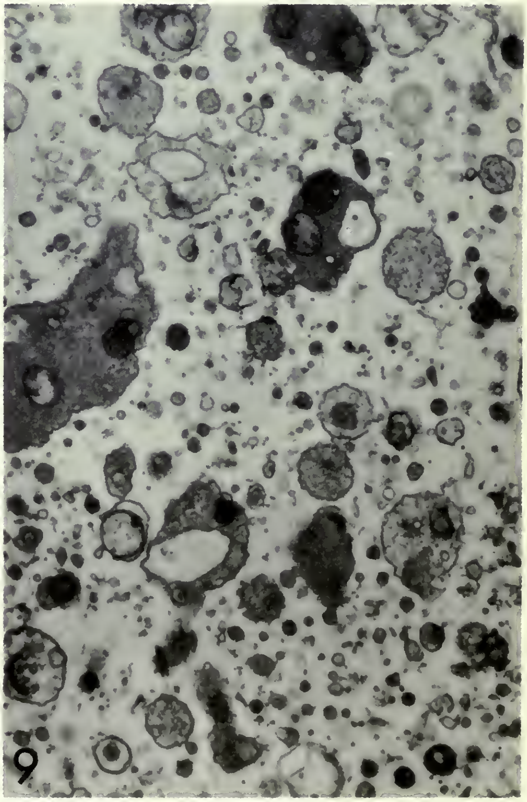


7

Fig. 7 Diagram showing a proposed pseudopodial network for *C. oviformis,* based on the examination of several micrographs.



8



9

Fig. 8 Section of the pseudopodial network of *Allogromia laticollaris* (Foraminifera), ×30 000.
Fig. 9 Section showing the size range of pseudopodial structures in *Shepheardella taeniformis* (Foraminifera), ×15 000.

and filose structures. We did not comment on them at the time, as there was insufficient information on the ultrastructural organization in other testate amoebae. It is now suggested that in *C. oviformis* the pseudopodial system is an anastomosing network. This appears to be so in other forms possessing filose pseudopodia, for example, *Euglypha* and *Trinema*, and also for some with lobose pseudopodia, for example, *Arcella*, *Centropyxis* and *Nebela* (unpublished observations). If this proves to be generally true of testate amoebae then the distinction between a filopodial system in such rhizopods and a reticulopodial system in foraminifera ceases to be valid. The difference remaining between the two groups would then be whether or not the network in testate amoebae is granular, as it clearly is in the foraminifera when viewed with the optical microscope (Hedley, 1964). At present the only report of granular filose pseudopodia in testate amoebae is that of Berrend (1966) who described the bi-directional flow of granules in *Cyphoderia ampulla*.

The ultrastructure of the pseudopodia of *C. oviformis* (Fig. 4) compares well with our previous studies of the fine structure of foraminifera, such as *Shepheardella taeniformis* (Fig. 9), *Allogromia laticollaris* (Fig. 8), *Iridia diaphana* and *Boderia turneri*, and with descriptions of foraminiferal pseudopodia by other workers (Wohlfarth-Botterman, 1961; Lengsfeld, 1969; Marsalek, 1969; Schwab, 1969; Febvre-Chevalier, 1971; Anderson & Bé, 1976, 1978).

The range in diameters of the pseudopodia in *C. oviformis* is 45 nm–3 μm and this compares favourably with those we have observed in foraminifera – *Allogromia laticollaris* 30 nm–2 μm, *Boderia turneri* 40 nm–1·5 μm, and *Iridia diaphana* 40 nm–2 μm – and those reported previously for the benthic foraminifer *Shepheardella taeniformis* 30 nm–1 μm (Hedley *et al.*, 1967) and the planktonic foraminifer *Globigerinoides sacculifera* 80 nm–2 μm (Anderson & Bé, 1978).

In conclusion it is suggested that the basic architecture of pseudopodial fine structure in testate amoebae supports the view that these forms produce a reticulopodium. In many characteristics they are similar to the reticulopodia found in foraminifera except that in the foraminifera the pseudopodia are invariably granular and exhibit bi-directional streaming when observed with the optical microscope.

References

Anderson, O. R. & Bé, A. W. H. 1976. The ultrastructure of a planktonic foraminifer, *Globigerinoides sacculifer* (Brady), and its symbiotic dinoflagellates. *J. foramin. Res.* **6** : 1–21.

—— —— 1978. Recent advances in foraminifera fine structure research. In *Foraminifera*, Vol. 3, R. H. Hedley & C. G. Adams (eds.). London, Academic Press, pp. 121–201.

Berrend, R. E. 1964. Filopodial movement in *Cyphoderia ampulla* (Ehr.). in *Primitive motile systems in cell biology*, R. D. Allen & N. Kamiya (eds). London, Academic Press, pp. 433–443.

Febvre-Chevalier, C. 1971. Constitution ultrastructurale de *Globigerina bulloides* d'Orbigny, 1826 (Rhizopoda – Foraminifera). *Protistologica* **7** : 311–324.

Hedley, R. H. 1964. The Biology of Foraminifera. In *The International Review of General and Experimental Zoology*, Vol. 1, W. J. L. Felts & R. J. Harrison (eds). London, Academic Press, pp. 1–45.

—— **Ogden, C. G. & Mordan, N. J.** 1977. Biology and fine structure of *Cryptodifflugia oviformis* (Rhizopodea : Protozoa). *Bull. Br. Mus. Nat. Hist.* (*Zool.*), 30 : 311–328.

—— **Parry, D. M. & Wakefield, J. St. J.** 1967. Fine structure of *Shepheardella taeniformis* (Foraminifera : Protozoa). *Jl. R. microsoc. Soc.*, **87** : 445–456.

Honigberg, B. M., Balamuth, W., Bovee, E. C., Corliss, J. O., Gojdicis, M., Hall, R. P., Kudo, R. R., Levine, N. D., Loeblich, A. R., Weiser, J. & Wenrich, D. H. 1964. A revised classification of the phylum Protozoa. *J. Protozool.* **11** : 7–20.

Leidy, J. 1879. Freshwater Rhizopods of North America. Report of the United States Geological Survey of the Territories, Washington, pp. 1–324.

Lengsfeld, A. M. 1969. Zum Feinbau der Foraminifere *Allogromia laticollaris*. II. Mitteilung : Ausgestreckte und durch Abreiben isolierte Rhizopodien. *Helgolander wiss. Meeresunters* **19** : 262–283.

Loeblich, A. R. & Tappan, H. 1961. Suprageneric classification of the Rhizopodea. *J. Paleont.* **35** : 245–330.

—— —— 1964. Thecamoebians. In *Treatise on Invertebrate Palaeontology*, Part C, Protista 2, Vol. 1. The Geological Society of America, University of Kansas Press, Lawrence, C16–C54.

Marsalek, D. S. 1969. Observations on *Iridia diaphana*, a marine foraminifer. *J. Protozool.* **16** : 599–611.

Page, F. C. 1975. A new family of amoebae with fine pseudopodia. *Zool. J. Linn. Soc.* **56** : 73–89.

—— 1976. An illustrated key to freshwater and soil amoebae with notes on cultivation and ecology. Freshwater Biological Association Scientific Publication No. 34, 1–155.

Saedeleer de, H. 1932. Reserches sur les pseudopodes des Rhizopodes Testacés. Les comcepts pseudopodes lobosa, filosa, et granulo-reticulosa. *Archs Zool. exp. gén.* **74** : 597–626.

Schwab, D. 1969. Electronenmikroskopische Untersuchung an der Foraminifere *Myxotheca arenilega* Schaudinn. *Z. Zellforsch* **96** : 295–324.

Wohlfarth-Bottermann, K. E. 1961. Cytologische Studien VIII. Zum Mechanismus der Cytoplasmastromung in dunnen Faden. *Protoplasma* **54** : 1–26.

Manuscript accepted for publication 7 February 1979

Review of the genus *Guaranidrilus* (Oligochaeta, Enchytraeidae) with the description of two new species

Brenda Healy

Zoological Department, University College, Dublin

Synopsis

Guaranidrilus Černosvitov, 1937 was erected to contain three new species from Argentina, *G. glandulosus*, *G. rarus* and *G. fridericoides* nom. nud. and a species of doubtful affinity, *G.* (*Henlea*) *columbianus* from Columbia. Only one other species, *G. lamottei* from Africa, has since been described. Although *G. fridericoides* was never described, re-examination of Černosvitov's specimens reveals that the species is distinctive. The genus is emended and two new species are described: *G. cernosvitovi* sp. nov. (for *G. fridericoides* nom. nud.) and *G. europeus* sp. nov. from France and Spain.

Introduction

The genus *Guaranidrilus* was erected by Černosvitov (1937*a*) to include four species: *G. glandulosus*, *G. rarus* and *G. fridericoides*, new species from Argentina; and *G. columbianus* (Michaelsen, 1913) from Columbia. The new species were not described at the time but subsequently descriptions were provided for two, *G. glandulosus* and *G. rarus*, together with a redefinition of the genus (Černosvitov, 1937*b*). The third, *G. fridericoides*, has never been described so the name does not fulfil the requirements of Article 13a of the International Code of Zoological Nomenclature and is considered to be a *nomen nudum*. Only one other species has been recorded, *G. lamottei* Omodeo, from the Ivory Coast (Omodeo, 1958). Recently new material of *Guaranidrilus* was collected from France and Spain and led to an investigation of the genus. Re-examination of Černosvitov's material of *G. fridericoides* in the British Museum (Natural History) showed that the species is distinct and a description is given in this paper together with details of a new species from S.W. France and the Pyrenees.

The three previously recorded localities of *Guaranidrilus* lie between 8° N and 27° S, thus the genus appears to have a mainly tropical distribution. Černosvitov (1937*b*) expressed the opinion that the genus is probably widely distributed in both tropical and subtropical parts of South America, although he presented no evidence to support this view. The discovery of a new species in south-west France and the Pyrenees is of special interest because it extends the known geographical range of *Guaranidrilus*. This new European species displays the essential characteristics of the genus but departs in two respects from Černosvitov's diagnosis: a seminal vesicle is absent and there are no oesophageal glands. Similarly *G. lamottei* also exhibits characters not shared with Černosvitov's species. The inclusion of these Old World species makes it necessary to emend the genus.

GUARANIDRILUS Černosvitov, 1937 (emended)

TYPE SPECIES. *G. glandulosus* Černosvitov, 1937 (designated by Brinkhurst & Jamieson, 1971).

DIAGNOSIS. Setae straight, without nodulus, two per bundle. Head pore at the tip of the prostomium; dorsal pores absent. Three pairs of septal glands united dorsally, all with ventral lobes. Sudden transition between oesophagus and intestine with a pair of bilobed intestinal diverticula at the oesophago-intestinal transition. Dorsal vessel originating in the clitellar region

Bull. Br. Mus. nat. Hist. (Zool.) **37** (1) : 7–15

Issued 29 November 1979

or just anterior to it. Interstitial tissue of the nephridia well developed; anteseptale large, containing coils of the canal, efferent duct terminal. Sperm funnel cylindrical, duct long and thin and wound into a spiral. Penial bulb compact. Spermatheca simple, not communicating with the oesophagus.

HABITAT. Terrestrial and freshwater.

SPECIES. *G. glandulosus*, *G. cernosvitovi* sp. nov. and *G. europeus* sp. nov. are distinctive species which cannot be confused with any of the enchytraeid species presently known and which fall clearly within the genus as defined. *G. columbianus* and *G. lamottei* are both incompletely described, there is therefore some doubt concerning their taxonomic affinities. *G. rarus* is close to *G. glandulosus* and the validity of the species is doubtful.

REMARKS. The intestinal diverticula have a characteristic bilobed shape which may be unique among the Enchytraeidae. Although diverticula occur at the oesophago-intestinal transition in *Buchholzia*, *Enchytronia* and some species of *Henlea*, these taxa differ from *Guaranidrilus* in possessing spermathecae which communicate with the oesophagus. Two characters which Černosvitov regarded as having generic significance have been omitted from the emended diagnosis: the presence of oesophageal glands (which he termed 'peptonephridia') and the presence of a seminal vesicle. Paired, spherical, oesophageal glands are present in VI in all three Argentinian species but in *G. lamottei* they originate at IV/V and are long and forwardly directed. Glands attached to the anterior part of the oesophagus have not been reported in *G. columbianus* and are probably absent as in *G. europeus*. This is seemingly a variable character as in *Marionina* and *Achaeta*. The seminal vesicle is variable in many enchytraeid genera. In *Fridericia*, for example, it is present in most species with large individuals but is absent from many of the species in which the worms are smaller.

SPECIFIC CHARACTERS. The main characters of the species are listed in Table 1. The most useful diagnostic characters are the presence and form of the oesophageal glands, the position of the intestinal diverticula, the size of the sperm funnel and seminal vesicle and the shape and size of the spermatheca. Černosvitov probably did not have access to live material and for this reason may have overemphasized the taxonomic importance of the position of the intestinal swelling and the shape and size of the intestinal diverticula. Examination of living specimens of *G. europeus* reveals that the intestinal diverticula are contractile and can vary in shape and size in an individual (Fig. 3). Also, the intestinal swelling appears to alter position according to the state of the diverticula, e.g. when the latter are expanded, the swollen region of the gut is pushed posteriorly. These characters are therefore unreliable for purposes of identification.

Guaranidrilus glandulosus Černosvitov, 1937

Guaranidrilus glandulosus Černosvitov, 1937*b* : 149, figs 1–9.

TYPE MATERIAL. Syntypes: 5 microslides (1 whole mount and 4 vertical longitudinal sections), British Museum (Natural History) Reg. Nos 1949.3.1.949–954. Collected 17.xi.31 and 18.ix.31; collector unknown.

Černosvitov stated that specimens were deposited in the Museo Argentino de Ciencias Naturales. The material referred to is probably that which is now in the collections of the British Museum (Natural History) (see *G. rarus*).

TYPE LOCALITY. Loreto, near Santa Ana, Misiones, Argentina. Soil rich in humus and stream detritus.

REMARKS. While Černosvitov's description is adequate, he gives no indication of the number of specimens examined or the extent of variation observed. The surviving material is, for the most part, poor, only one of the preparations shows the diagnostic characters clearly. It seems probable that the description was based on a small number of specimens giving a somewhat narrow concept of the species. Some variation is to be expected, especially in the size of the intestinal diverticula.

Table 1 The species of *Guaranidrilus:* distinguishing characters

	G. glandulosus	*G. cernosvitovi* sp. nov.	*G. europeus* sp. nov.	*G. columbianus*	*G. lamottei*	*G. rarus*
Size (in mm)	5–7	12–13	2–4	4·5–6·5	*c.* 10	2·5–3
Segments	30–35	47–48	23–29	35–40	57–58	33
Setae, presence (2 per bundle)	throughout	throughout	throughout	throughout	dorsal bundles absent from VIII	throughout
Cutaneous glands	distinct, 6–8 rows	indistinct	indistinct, 4–5 rows	indistinct	?	absent
Clitellar glands, arrangement	regular rows	regular rows	regular rows	regular rows	?	regular rows
Head pore, location	tip of O	tip of O	tip of O	tip of O	O/I	tip of O
Oesophago-intestinal transition	mid VIII	VII/VIII	VII/VIII	IX/X?	VII/VIII	Post part of VII
Intestinal diverticula						
communicating in	VIII	VII	VII/VIII	VII/VIII	VII/VIII	VII
occupying	VII, VIII, IX	VII, VIII	VII, VIII	VII, VIII (IX)	VII	VII
Oesophageal glands	dorsal in VI	dorso-lateral in VI	absent	absent	originating in IV, long, directed ant.	ventral in VI
Origin of dorsal vessel	XII/XIII	X/XI	XII/XIII	X	XII/XIII	X/XI
Brain	cleft	cleft	cleft	cleft	nearly straight	cleft
length : width	1·5	?	2	1·5	1·5	?
Sperm funnel						
length : width	1·5	4–5	1·5	2	?	1·5
Seminal vesicle	medium size	very large	absent	absent	?	medium size
Spermatheca:						
ampulla	free, in VII	free, in VII–IX	free, in VI	communicating ?	free (immature)	free, in VI
duct	thin-walled, ectal swelling	thick-walled, no ectal swelling	thin-walled, slight swelling	ectal swelling ?	?	thin-walled, no distinct swelling
ectal glands	absent	absent	absent	small	?	absent

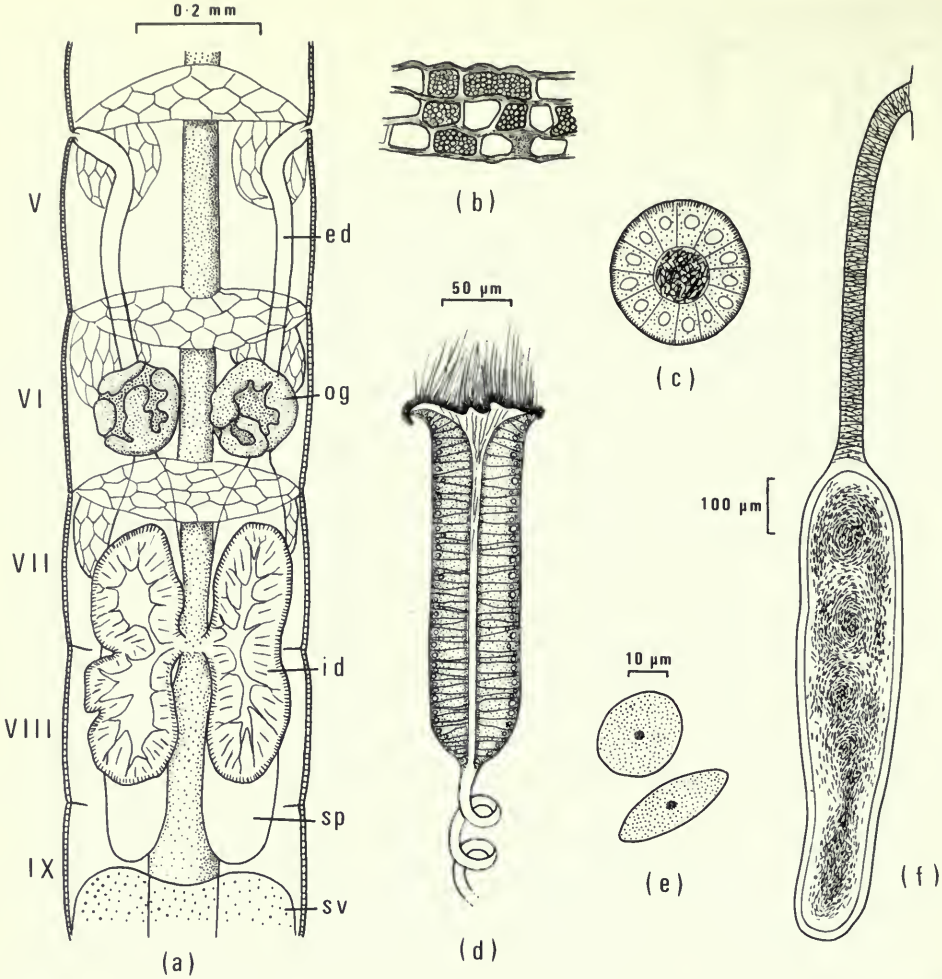


Fig. 1 *Guaranidrilus cernosvitovi* sp. nov.: (a) Segments V–IX. *ed* – ectal duct of spermatheca, *og* – oesophageal gland, *id* – intestinal diverticulum, *sp* – spermathecal ampulla, *sv* – seminal vesicle; (b) Clitellar glands; (c) Transverse section of ectal duct; (d) Sperm funnel and part of duct; (e) Lymphocytes; (f) Spermatheca.

Guaranidrilus cernosvitovi sp. nov.

Guaranidrilus fridericoides nom. nud. Černosvitov, 1937*a* : 282.

Description. Length (preserved specimens) 12–13 mm, width 0·4–0·5 mm. Segments 47–48 (6 specimens). Setae straight with weak ental hook, approximately equal, 50–60 µm. Cutaneous glands indistinct. Clitellum extending over XII–$\frac{1}{2}$XIII with squarish glands arranged in transverse rows (Fig. 1b). Head pore at the tip of the prostomium. Three pairs of septal glands, all with ventral lobes and united dorsally. Brain incised posteriorly. Transition between oesophagus and intestine not sudden, represented by a slight enlargement at VII/VIII. A pair of more or less spherical glands attached to the oesophagus dorso-laterally in VI, 80–100 µm in diameter, highly vascularized (Fig. 1a). Paired, hollow, bilobed intestinal diverticula in VII, 230 µm in length, their point of attachment just in front of the oesophago-intestinal transition (Fig. 1a). Chlorogogen cells about the same size as the lymphocytes or a little smaller. Lymphocytes nucleated, finely granulated, 25–35 µm, mostly spindle-shaped, sometimes oval or circular

(Fig. 1e). Nephridia all with a large anteseptal portion about one-third the total length of the nephridium; efferent duct terminal, short. Origin of dorsal vessel at X/XI.

Sperm funnel large, 350 µm in length, width varying between 75 and 200 µm with a wide, much-lobed collar (Fig. 1d). Sperm duct long and coiled into a spiral. Seminal vesicle very large, occupying IX–XI. Penial bulb small. Spermatheca large with a thick-walled ectal duct (Fig. 1c) extending through V and VI and a large cylindrical ampulla, 150–230 µm in diameter, extending through VII and VIII (Fig. 1f). Ectal glands absent.

TYPE MATERIAL. Holotype: 1 microslide (unstained whole mount prepared by the author), British Museum (Natural History) Reg. No. 1949.3.1. Collected 12.vi.32; collector unknown. Paratypes: 3 microslides (whole mounts), 3 microslides (vertical longitudinal sections), 2 microslides (transverse sections), British Museum (Natural History) Reg. Nos 1949.3.1b–i. Spirit material (about 17 specimens).

TYPE LOCALITY. Loreto, near Santa Ana, Misiones, Argentina. Habitat unknown.

REMARKS. The species is well defined and readily distinguished by its large size and large sexual organs, i.e. sperm funnels, seminal vesicle and spermathecae. There appears to be little variation in segment number or in the form of the internal organs.

It is not evident why Černosvitov failed to describe so distinctive a species, especially as more material was available to him than for either *G. glandulosus* or *G. rarus*. Two of the microslides in his collection (longitudinal and transverse sections) are excellent and show most diagnostic characters clearly.

Guaranidrilus europeus sp. nov.

DESCRIPTION. Small species, length 3–6 mm, width 100–140 µm. Segments 23–29. Setae straight with weak ental hook, two per bundle throughout, approximately equal, about 20 µm (Fig. 2d). Setae absent in XII. Occasional single setae in the coelom. Cutaneous glands indistinct, elongated, 3–5 rows per segment (Fig. 2a). Clitellum extending over XII/½XIII with 20–33 rows of squarish glands (Fig. 2b). Head pore near the tip of the prostomium. Three pairs of septal glands, all united dorsally and with ventral lobes (Fig. 2h). Brain about twice as long as broad, the posterior margin deeply cleft (Fig. 2e). Sudden transition between oesophagus and intestine usually at VII/VIII but the position can vary according to the state of the intestinal diverticula. When these are expanded, the intestine may be constricted so that the swelling appears in IX. The two lateral intestinal diverticula communicate at VII/VIII and extend both forwards and backwards (Fig. 3a). They usually measure 150–160 µm and occupy VII and VIII but may extend anteriorly into VI and posteriorly into XI. They are hollow and highly contractile but do not pulsate; some variations in shape are shown in Fig. 3. Chlorogogen cells about the same size as the setae. Lymphocytes circular or oval, finely granular and nucleated, 10–20 µm (Fig. 2c). Nephridia similar throughout, the anteseptal portion large with coils on the canal, the efferent duct terminal (Fig. 2i). Dorsal vessel originating in XII or XIII, blood colourless.

One or two mature eggs present at a time. Sperm funnel pear-shaped, about 1½ times longer than wide, length 40 µm (Fig. 2g). Sperm duct long and coiled. Seminal vesicle absent. Spermatheca free, its length 2–2½ times the diameter of the worm. The thin-walled ectal duct has small scattered gland cells. It expands gradually into a terminal ampulla in VI. There is a slight expansion of the ectal duct near its orifice but no ectal glands (Fig. 2f).

The description is based entirely on live specimens. The worms were transparent when viewed microscopically and all characters could be readily observed. Thirty-two specimens were examined from two widely separated populations; intraspecific variation appears to be slight.

TYPE MATERIAL. Holotype: 1 microslide (whole mount) British Museum (Natural History) Reg. No. 1978.39.1. Collected by the author 21.x.77. Paratypes: 1 microslide (whole mount), British Museum (Natural History) Reg. No. 1978.39.2. 2 microslides (whole mounts), Museum

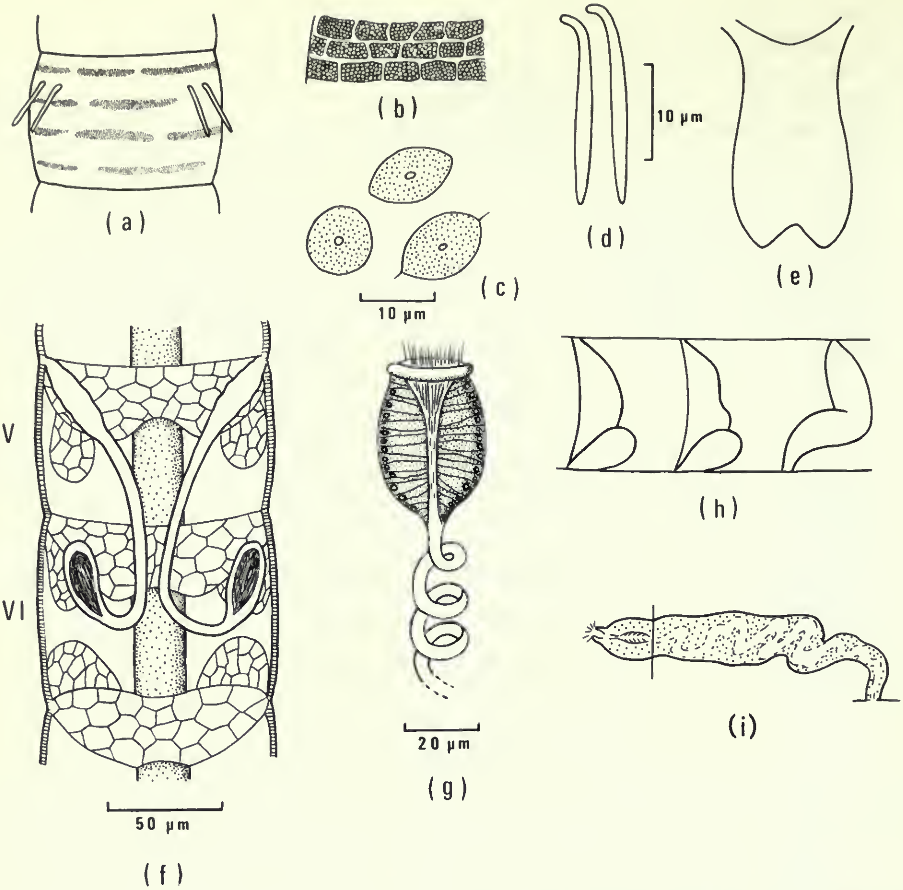


Fig. 2 *Guaranidrilus europeus* sp. nov.: (a) Preclitellar segment showing cutaneous glands; (b) Clitellar glands; (c) Lymphocytes; (d) Setae; (e) Brain; (f) Segments V–VI showing septal glands and spermathecae; (g) Sperm funnel and part of duct; (h) Septal glands, lateral view; (i) Nephridium.

National d'Histoire Naturelle, Paris, Reg. Nos AP 700–701. 7 microslides (whole mounts) and 5 specimens fixed in Bouin's in the author's collection. Collected by the author 21.x.77.

TYPE LOCALITY. Near Arcachon, S.W. France. Beside a small pond in a pine-wood clearing at the edge of the road from Le Corneau to Pilat. Wet sandy peat and peaty sand, pH 4·0–5·7.

OTHER MATERIAL EXAMINED. 9 specimens from Roncesvalles, Spanish Pyrenees, collected 31.vii.75. Marshy pasture, wet–very wet, pH 6·0–7·2. 1 Specimen from a pasture near Arcachon, S.W. France, collected 6.vii.75. Moist sandy loam, pH 5·9–6·1.

REMARKS. The diagnostic characters of the species are its small size and the absence of both oesophageal glands and seminal vesicle.

Since it is unlikely that so distinctive a species could have been overlooked in northern Europe where the Enchytraeidae are quite well known, this new species is presumably confined to the south where it may represent a sub-tropical element in the European fauna. The enchytraeid fauna of southern Europe has received little attention; the only well-studied regions are northern Italy and Romania where *Guaranidrilus* has not been found. Hence, the genus may be confined to south-west Europe being representative of a Lusitanian fauna. In south-west France, *G. europeus* is rare. In July–August 1975 and October 1977 collections were made at 37 localities

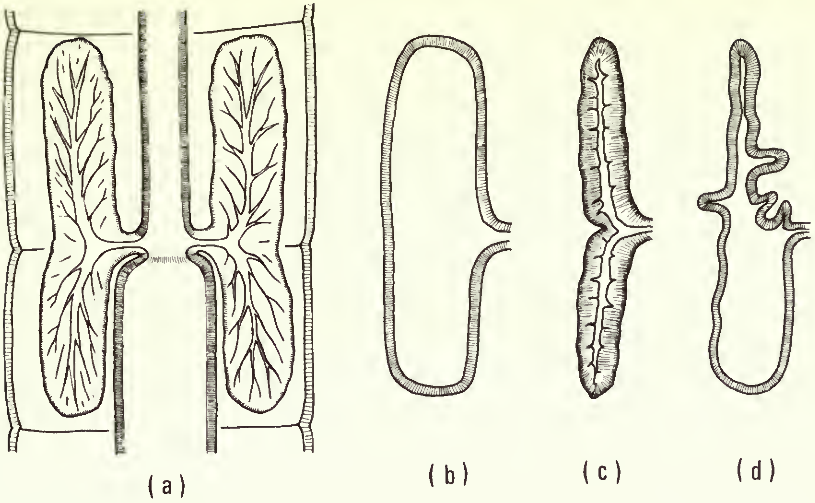


Fig. 3 *Guaranidrilus europeus* sp. nov.: (a) Intestinal divicula and oesophago-intestinal transition; (b)–(d) Various forms of the intestinal diverticula.

in the Landes, 12 in the Dordogne region and 11 in the Atlantic Pyrenees but *G. europeus* was found at only two sites. At the type locality the population was small and restricted to the edge of a small pond. At the other locality, only one specimen was found in spite of much searching. The population in the Spanish Pyrenees, discovered in July 1975, also appeared to be very localized. In October 1977, no specimens could be found at this locality. Generally, the enchytraeid fauna of Spain and Portugal is poorly known. Before the status of *G. europeus* can be established in Europe, it will be necessary to collect extensively in these regions and in the Mediterranean region of France.

Guaranidrilus columbianus (Michaelsen, 1913)

Henlea columbiana Michaelsen, 1913 : 211.

Type material. Syntypes: 2 spirit specimens (1 mature, 1 immature), Zoologisches Museum, Hamburg, Reg. No. V 7739. Collected by O. Fuhrmann, date unknown.

Type locality. Medellin, Medellin Lake at Ufer, Colombia. Altitude 2000 m. Habitat unknown.

Remarks. Michaelsen's description, although covering the principal features, is imprecise in places and is not illustrated, hence the species is not clearly defined. He referred it to the genus *Henlea* on the morphology of the oesophago-intestinal transition which he observed just behind the septum in X with the dorsal vessel also originating in this position and large, hollow 'peptonephridia' in VII–IX. The spermathecae were seen to communicate with the oesophagus, a characteristic feature of *Henlea*. However, Černosvitov (1937*b*) considered that many features such as setal number, brain, septal glands, clitellar glands and spirally coiled sperm duct, linked the species with *Guaranidrilus* and that the 'peptonephridia' in VII–IX were in fact similar to the intestinal diverticula of *G. glandulosus*. He also observed that in *Guaranidrilus* the spermathecal ampulla often adheres to the oesophagus making it difficult to trace the spermatheca over its entire length, he concluded that Michaelsen may have been mistaken in his interpretation of this organ. In support of this view it is worth noting that Michaelsen seems to have experienced difficulty in distinguishing both spermathecae and 'peptonephridia' because he states that in one serially sectioned specimen the 'peptonephridia' appeared to extend forward as a narrow tube into V, terminating close to the opening of the spermathecal duct. It seems more likely that the tube was actually the spermathecal duct and that the spermathecal ampulla was not developed, as, for example, in an unfertilized specimen.

A re-examination of Michaelsen's type material led to the conclusion that Černosvitov was correct in placing the species in *Guaranidrilus*. Although the attachment of the intestinal diverticula could not be clearly seen in either of the specimens, the organs are more similar in general appearance to those of other members of the genus than to those of the known species of *Henlea*. Unfortunately, the proximal regions of the spermathecae were not distinct in the single mature specimen so the uncertainty concerning the communication with the oesophagus remains. It was possible, however, to see the nephridia which Michaelsen did not describe fully. They are clearly of the *Guaranidrilus*-type with a large anteseptale consisting of nephrostome surrounded by coils of the canal and a terminal efferent duct, quite different from the *Henlea*-type in which the anteseptale consists of nephrostome only and the efferent duct originates in the anterior position just behind the septum.

From the information available, the distinguishing characters of *G. columbianus* are its size, the absence of oesophageal glands and seminal vesicle and the position of the intestinal diverticula and oesophago-intestinal transition. In both type specimens the intestinal transition is at VIII/IX, not at IX/X as stated by Michaelsen. However, the specimens are somewhat contracted and there may have been displacement of some organs. In the immature specimen, intestinal diverticula on both sides are confined to VII and VIII but in the mature specimen one of the sacs occupying VIII extends back into IX. There may therefore be variations in the size of the diverticula.

Guaranidrilus lamottei Omodeo, 1958

Guaranidrilus lamottei Omodeo, 1958 : 11, fig. 1.

Type material. Not located. Collected 8–9.viii.51.

Type locality. Zouguépo, Mount Nimba, Ivory Coast. Path in mountain grassland, 1360 m.

Remarks. The description was based on immature specimens only and is thus incomplete. The author referred the species to *Guaranidrilus* with some hesitation noting that several features such as the position of the head pore at O/I and the ciliated inner surface of the intestinal diverticula are more characteristic of the *Henlea* group. There may be some doubt about the position of the head pore since the author admitted that it was barely perceptible. The bilobed diverticula at the oesophago-intestinal transition, the nephridia with terminal efferent ducts, the presence of free spermathecae and coiled sperm ducts are characteristic of *Guaranidrilus*.

G. lamottei possesses some unusual features not shown by other members of the genus, notably the absence of dorsal setae in all segments posterior to VIII and the length and point of attachment of the oesophageal glands. The almost straight posterior border of the brain also distinguishes it from other species. In view of these pecularities and the immaturity of the specimens, the systematic position of the species must remain uncertain.

Guaranidrilus rarus Černosvitov, 1937

Guaranidrilus rarus Černosvitov, 1937*b* : 151, figs 10–15.

Type material. Syntypes: 2 microslides (1 whole mount and 1 of horizontal longitudinal sections), British Museum (Natural History), Reg. Nos 1949.3.1.954–955. Collected 21.xii.31; collector unknown.

Černosvitov (1937*b*) noted that only two mature specimens were found. As the two specimens in the British Museum (Natural History) collection must therefore represent the entire material underlying the description, it is evident that Černosvitov did not deposit the specimens in the Museo Argentino as he stated.

Type locality. Loreto, near Santa Ana, Misiones, Argentina. Under the bark of an old tree.

Remarks. Černosvitov distinguished *G. rarus* from *G. glandulosus* on the position of the intestinal dilatation in VII and not in VIII, the smaller size of the intestinal diverticula, the origin of the dorsal vessel at X/XI instead of at XII/XIII and the absence of cutaneous glands. The size of the intestinal diverticula cannot be considered significant in view of the contractile nature of these organs while the position of the intestinal swelling may also be variable. A more reliable taxonomic character is the position of attachment of the intestinal diverticula – clearly seen in the longitudinal sections. This character, together with the point of origin of the dorsal vessel, could be sufficient to delineate this species but since observations were made on only two specimens, the consistency of these characters cannot be considered proven. The small size of the specimens may be diagnostic but it is possible that this is due to ecological factors such as low moisture content. The segment number falls within the range of *G. glandulosus* (Table 1) and both oesophageal glands and spermathecae are similar in the two species. In view of these similarities, the lack of reliable diagnostic characters and the paucity of material, the validity of the species must be considered doubtful.

Acknowledgments

My thanks go to R. W. Sims of the British Museum (Natural History) for his co-operation and for advice on nomenclature and taxonomic problems. Part of this work was carried out during two surveys of French Enchytraeidae during which I stayed at the Station Biologique, Arcachon. I wish to thank all those who made my visits so pleasant and particularly Pierre and Bernadette Lasserre for their kindness. The surveys were funded jointly by the Centre National de la Recherche Scientifique and the National Science Council of Ireland whose support is gratefully acknowledged.

References

Brinkhurst, R. O. & Jamieson, B. G. M. 1971. *Aquatic Oligochaeta of the World.* Edinburgh, Oliver & Boyd, pp. 1–860.

Černosvitov, L. 1937*a*. System der Enchytraeiden. *Zap. nauchno-issled. Ob'ed. russk. svob. Univ. Praga* **5** (10) (Sci. nat. Mat.) No. 34 : 263–295.

—— 1937*b*. Notes sur les Oligochaeta (Naididées et Enchytraeidées) de l'Argentine. *An. Mus. argent. Cienc. nat.* **39** : 135–157.

Michaelsen, M. 1913. Die Oligochaeten Columbias. *Mém. Soc. neuchat. Sci. nat.* **5** : 202–253.

Omodeo, P. 1958. La reserve naturelle intégrale du Mont Nimba. IV. 1. Oligochètes. *Mém. inst. fr. Afr. noire* **53** : 9–17.

Manuscript accepted for publication 26 January 1979

Larval development of British prawns and shrimps (Crustacea : Decapoda : Natantia). 3. *Palaemon (Palaemon) longirostris* H. Milne Edwards, 1837 and the effect of antibiotic on morphogenesis

A. A. Fincham

Department of Zoology, British Museum (Natural History), Cromwell Road, London SW7 5BD

Synopsis

The larval stages of *Palaemon* (*Palaemon*) *longirostris* are described from specimens reared in the laboratory with (+AB) and without (−AB) antibiotics. Growth in the early stages of larval development was enhanced by the use of antibiotics. There was also an increase in intermoult period and a two-moult delay of metamorphosis from 7 to 9 in +AB larvae. With these exceptions, the effect of antibiotics on morphogenesis was no more than expected in normal meristic variation. The relationship between moulting, growth and morphogenesis is examined in relation to genetic input, epigenesis and phenotypic variation in this estuarine species.

Introduction

The aim of this paper is twofold: to provide a complete description of the larval development of *Palaemon* (*Palaemon*) *longirostris* H. Milne Edwards, 1837 including the hitherto unknown zoea 4 and to assess both quantitative and qualitative effects of antibiotics on morphogenesis. Little attention has been given to the larval development of *P.* (*P.*) *longirostris* with the exception of papers by Gurney (1924*b*) and Korshelt (1944) in which zoeae 1–3, 5 and post larvae were described. The adults of this species are widely distributed in estuaries (Gurney, 1923; De Man, 1923) with records from the southern North Sea, west coast of Ireland and as far south as the Bay of Biscay (Fincham & Williamson, 1978). The species is also present in the Mediterranean and Black Seas. Larvae from plankton samples, however, are extremely rare (Gurney, 1924*b*; Williamson, personal communication). Personal observations on offshore, inshore and estuarine plankton samples which were collected from the North Sea and around the English and Welsh coasts by MAFF Fisheries Laboratory, Lowestoft, confirm these earlier findings.

Antibiotics are used routinely in the culture of larval decapods at the BM(NH) as an additive to the sea water to control build-up of bacteria in the compartmented rearing trays (Fincham, 1977, 1979). The effect of antibiotics on the development of brachyuran decapods has been investigated (Christiansen, 1971) but their effect on morphogenesis in natant decapods is less well known. Wickins (1972) compared the survival of *Palaemon serratus* (Pennant, 1777) larvae and the proportion which metamorphosed when cultured with and without antibiotics.

Materials and methods

Ovigerous *Palaemon* (*Palaemon*) *longirostris* were collected in July 1977 from filtering screens at the tidal water intake of the West Thurrock Electricity Generating Station on the River Thames (grid reference: TQ 593768). Rearing techniques similar to those reported previously (Fincham, 1977, 1979) were used with the following modifications:

1. The controlled temperature room was at 18 ± 0·5 °C, equivalent to ambient water temperature at the time of collection.

Bull Br. Mus. nat. Hist. (Zool.) **37** (1) : 17–46

Issued 29 November 1979

Table 1 Larval development and the effect of antibiotic on morphological variation in *Palaemon* (*Palaemon*) *longirostris*. (Figures in brackets refer to larvae reared with antibiotic.)
R = rudimentary; + = present/yes; − = absent/no

	Zoea/Moult							
	1	2	3	4	5	6	7	PL1(8)
Carapace								
No. of dorsal spines	0 (0)	1 (1)	2 (2)	3 (3)	3 (3)	3 (3)	3 (3)	6 (3)
No. of ventral rostral spines	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0–1 (0–1)	2 (0–1)
Supraorbital spines +/−	− (−)	+ (+)	+ (+)	+ (+)	+ (+)	+ (+)	+ (+)	− (+)
No. of antero-lateral spines	0 (0)	1 (1)	2 (2)	2 (2)	2 (2)	2 (2)	2 (2)	2 (2)
Rostrum tip – downturned +/−	− (−)	+ (+)	+ (+)	+ (+)	+ (+)	+/− (+/−)	+/− (+/−)	− (+/−)
Ventral retrorse hooks +/−	+ (+)	+/− (+/−)	+/− (+/−)	− (−)	− (−)	− (−)	− (−)	− (−)
	one group				two groups			
Antenna 1								
No. of aesthetascs	1 Wide 2 narrow (,,)	2 Wide 2 narrow (,,)	3 Wide (,,)	3 Wide 1 narrow (,,)	3 Wide + 1 narrow; 2 narrow (,,)	4 Wide; 2 Wide (,,)	4 Wide; 2 Wide (,,)	3 Wide; 2 Wide (,,)
Stylocerite +/−	− (−)	R (R)	+ (+)	+ (+)	+ (+)	+ (+)	+ (+)	+ (+)
Statocyst +/−	− (−)	− (−)	− (−)	R (R)	+ (+)	+ (+)	+ (+)	+ (+)
No. of segments, flagellum – Internal	0 (0)	(0) (0)	1 (1)	1 (1)	1 (1)	2 (2)	3 (3)	6–9 (3)
External	1 (1)	1 (1)	1 (1)	1 (1)	1 (1)	1 (1–2)	2 (2)	6 (2)
Accessory flagellum +/−	− (−)	− (−)	− (−)	− (−)	− (−)	− (−)	− (−)	R (−)
Antenna 2								
Endopodite – No. of segments	1 (1)	1 (1)	3 (3)	5 (5)	6–8 (6–8)	9–10 (9–15)	12–16 (13–15)	44+ (13+)

Length of scaphocerite	1 : 1·4	1 : 1·2	1 : 0·9	⩽	<	<	<	<
	(1 : 1·4)	(1 : 1·2)	(1 : 0·9)	(⩽)	(<)	(<)	(<)	(<)
Exopodite – No. of distal segments	5	4–5	3	0	0	0	0	0
	(5)	(4–5)	(3)	(0)	(0)	(0)	(0)	(0)
No. of plumose setae	9+2	16+2–17+2	20+2–21+2	22+2–23+2	26–28	27–29	29–30	36–38
	(9+2)	(16+2)	(20+2)	(,,)	(25+27)	(26–30)	(29–30)	(31–33)
External spine +/–	–	–	–	+	+	+	+	+
	(–)	(–)	(–)	(+)	(+)	(+)	(+)	(+)
Mandible – Lacinia mobilis +/–	+	+	+	+	+	+	+	–
	(+)	(+)	(+)	(+)	(+)	(+)	(+)	(–)
Palp	–	–	–	–	–	–	–	–
	(–)	(–)	(–)	(–)	(–)	(–)	(–)	(–)
Maxilla 1								
No. of endite setae – Coxa	6	6	6	7	7	8	8	8–9
	(6)	(6)	(6)	(7)	(7)	(8)	(8)	(8)
Basis	5	7	7	7–8	(8)	8	8	14–16
	(5)	(7)	(7)	(7–8)	(8)	(8)	(8–9)	(8–9)
Maxilla 2								
No. of endite setae – Coxa	4	4	4	4	4	4	4	0
	(4)	(4)	(4)	(4)	(4)	(4)	(4)	(4)
Basis 1	3	3	3	3	3	3	4	6–7
	(3)	(3)	(3)	(3)	(3)	(3)	(4)	(4)
Basis 2	4	4	4	4	4	4	4	8
	(4)	(4)	(4)	(4)	(4)	(4)	(4–5)	(4–5)
Endopodite	3	3	3	3	3	3	3	1
	(3)	(3)	(3)	(3)	(3)	(3)	(3)	(3)
No. of plumose setae – Exopodite	5	7	9–11	12–13	(19–20)	22–25	25–28	30–33
	(5)	(7)	(10–11)	(15–17)	(17–22)	(24–26)	(25–28)	(27–28)
Maxilliped 1								
No. of setae on internal margin – Coxa	1	1	1	1	1	1	1	6–7
	(1)	(1)	(1)	(1)	(1)	(1)	(1)	(1)
Basis	6	6	6	6	6	7	7–8	27–30
	(6)	(6)	(6)	(6)	(6)	(7)	(7–8)	(7–8)
Exopodite – No. of proximo-lateral setae	0	0	0	0	0	3	5–6	8–9
	(0)	(0)	(0)	(0)	(0)	(4)	(5–6)	(6)
Maxilliped 2								
Endopodite – No. of segments	4	4	4	4	4	4	4	5
	(4)	(4)	(4)	(4)	(4)	(4)	(4)	(4)

Table 1 (*cont.*)

	Zoea/Moult							
	1	2	3	4	5	6	7	PL1(8)
Exopodite +/−	+	+	+	+	+	+	+	+
	(+)	(+)	(+)	(+)	(+)	(+)	(+)	(+)
Setae +/−	+	+	+	+	+	+	+	+
	(+)	(+)	(+)	(+)	(+)	(+)	(+)	(+)
Maxilliped 3								
Endopodite – No. of segments	4	5	5	5	5	5	5	4
	(4)	(5)	(5)	(5)	(5)	(5)	(5)	(5)
Exopodite +/−	+	+	+	+	+	+	+	R
	(+)	(+)	(+)	(+)	(+)	(+)	(+)	(+)
Setae +/−	+	+	+	+	+	+	+	+
	(+)	(+)	(+)	(+)	(+)	(+)	(+)	(+)
Pereiopods 1 & 2 +/−	R	+	+	+	+	+	+	+
	(R)	(+)	(+)	(+)	(+)	(+)	(+)	(+)
Biramous +/−	+	+	+	+	+	+	+	R
	(+)	(+)	(+)	(+)	(+)	(+)	(+)	(+)
Endopodite – Propodus fixed finger +/−	−	−	+	+	+	+	+	+
	(−)	(−)	(+)	(+)	(+)	(+)	(+)	(+)
Pereiopod 3 +/−	R	R	R	+	+	+	+	+
	(R)	(R)	(R)	(+)	(+)	(+)	(+)	(+)
Biramous +/−	+	+	+	+	+	+	+	R
	(+)	(+)	(+)	(+)	(+)	(+)	(+)	(+)
Pereiopod 4 +/−	R	R	R	+	+	+	+	+
	(R)	(R)	(R)	(+)	(+)	(+)	(+)	(+)
Biramous +/−	−	−	−	−(R)	−	−	−	−
	(−)	(−)	(−)	(−)	(−)	(−)	(−)	(−)

Pereiopod 5 +/−	R	R	+	+	+	+	+	+
	(R)	(R)	(+)	(+)	(+)	(+)	(+)	(+)
Biramous +/−	−	−	−	−	−	−	−	−
	(−)	(−)	(−)	(−)	(−)	(−)	(−)	(−)
Abdomen								
Somite 5 – lateral spines +/−	−	+	+	+	+	+	+	R
	(−)	(+)	(+)	(+)	(+)	(+)	(+)	(+)
Somite 6 – ‘Continuous’ with telson +/−	+	+	−	−	−	−	−	−
	(+)	(+)	(−)	(−)	(−)	(−)	(−)	(−)
Pleopods +/−	−	−	R	R	R	R	R	+
	(−)	(−)	(R)	(R)	(R)	(R)	(R)	(R)
Fringing setae			−	−	−	−	R	+
			(−)	(−)	(−)	(−)	(R)	(R)
Appendix interna 2–5 +/−			−	−	−	R	+	+
			(−)	(−)	(−)	(R)	(+)	(+)
Telson								
Posterior margin concave (−) or	+/−	+/−	(−)	−	−	+/−	+/−	+
convex (+)	(+/−)	+/−	(−)	(−)	(−)	(+/−)	(+/−)	(+/−)
Spine formula	7+7	7+7	[1]6+6[1]	[1]6+6[1]	[3]4+4[3]	4+4	4+4	2+2
	(7+7)	(7+7)	([1]6+6[1])	(,,)	(,,)	(,,)	(,,)	(4+4)
Small spines +/−	+	+	+	+	+	+/−	−	−
	(+)	(+)	(+)	(+)	+	(+/−)	(−)	(−)
No. of pairs of lateral spines	0	0	0	0	0	3	3	3
	(0)	(0)	(0)	(0)	(0)	(3)	(3)	(3)
Uropods +/−	−	−	+	+	+	+	+	+
	(−)	(−)	(+)	(+)	(+)	(+)	(+)	(+)
Long plumose setae – Endopodite			0	12–13	17–19	20–21	23–26	28–31
			(0)	(12–13)	(17–20)	(20–25)	(20–25)	(24–26)
Exopodite			12–13	18+1−	20+1−	24+1−	26+1−	29–30
				20+1	23+1	26+1	28+1	
			(12+13)	(19+1	(21+1	(25+1	(25+1	(26+1
				−20+1)	−25+1)	−28+1)	−28+1)	−28+1)

2. Salinity of the water in the circulating system and the water used in the compartmented trays was adjusted to the conditions prevailing in the estuary (salinity varied from 10 to 17‰ at West Thurrock – laboratory salinity maintained at 14‰).
3. In 6 rearing trays, each with 18 compartments, a mixture of 50 i.u. benzylpenicillin (sodium) and 0·05 mg streptomycin sulphate per ml sea water was used instead of streptomycin sulphate alone.
4. A replicate series of trays was set up with no antibiotic in the sea water. The length of intermoult period, growth rate and meristic characters could then be compared with larvae reared with antibiotics.

Larval material has been deposited in the Crustacea collection of the BM(NH), registration number 1978: 307.

Palaemon* (*Palaemon*) *longirostris H. Milne Edwards, 1837

Palaemon longirostris H. Milne Edwards, 1837.
Palaemon edwardsii Heller, 1863.
Leander edwardsii Czerniavsky, 1884.
Leander longirostris De Man, 1915.
Leander longirostris Gurney, 1924*b*.
Palaemon (*Palaemon*) *longirostris* Holthuis, 1950.

SYNOPSIS OF LARVAL DATA FROM PUBLISHED WORK. *Leander longirostris* Gurney, 1924*b*: Figs 1–7 (zoeae 1–3, 5, post larvae 1, 2) laboratory reared and plankton; *Leander longirostris* Korschelt, 1944: Figs 810, 811 (zoeae 1–3) (after Gurney).

In the following short descriptions of the key characters of the larval stages, all setal counts have been omitted but these are recorded in Table 1.

DESCRIPTION OF LARVAL STAGES

Key characters are printed in *italic type* and are useful for separating stages of British species.

ZOEA 1 (Fig. 1) 3·5 mm (3·3–3·8 mm)*.

Head (Figs 1a, b): *eyes sessile.*

Carapace (Figs 1a, b): *without spines*, rostrum straight, tapering distally, ventral margin with minute retrorse teeth distally; *rostrum as long as or longer than antenna 1* (excluding terminal aesthetascs and setae).

Antenna 1 (Fig. 1c): peduncle bearing single flagellar segment, with three aesthetascs distally, one wide and two narrow.

Antenna 2 (Fig. 1d): exopod as a broad lamina divided into 5 (occasionally 6) segments distally; *endopodite of 1 segment.*

Mandibles (Fig. 1e): asymmetrical.

Maxillipeds 1–3 (Figs 1h–j): with natatory exopods.

Pereiopods 1, 2 (Figs 1k, l): *rudimentary, biramous.*

Pereiopod 3 (Fig. 1m): *minute biramous bud.*

Pereiopods 4, 5 (Figs 1n, o): minute uniramous buds.

Abdomen (Figs 1a, b): *somite 5 with posterior margin rounded*, not produced into spines; somite 6 continuous with telson. No trace of pleopods.

Telson (Figs 1p, q): fans out distally, posterior margin bears 7+7 plumose spines, inner pairs with longitudinal rows of scale-like spinules, decreasing in size on the plumose setae towards the edge of the fan; minute spines between four innermost pairs of plumose setae.

ZOEA 2 (Fig. 2) 3·9 mm (3·8–4·1 mm)

Head (Figs 2a, b): *eyes stalked.*

Carapace (Figs 2a, b): *one dorso-medial and a pair of supraorbital spines* all bent forward with small retrorse teeth, *rostrum without teeth, downturned at end to form a small hook.*

---

* Lengths of larvae reared without antibiotic quoted throughout; for comparison of larval growth rates with and without antibiotic see Fig. 18.

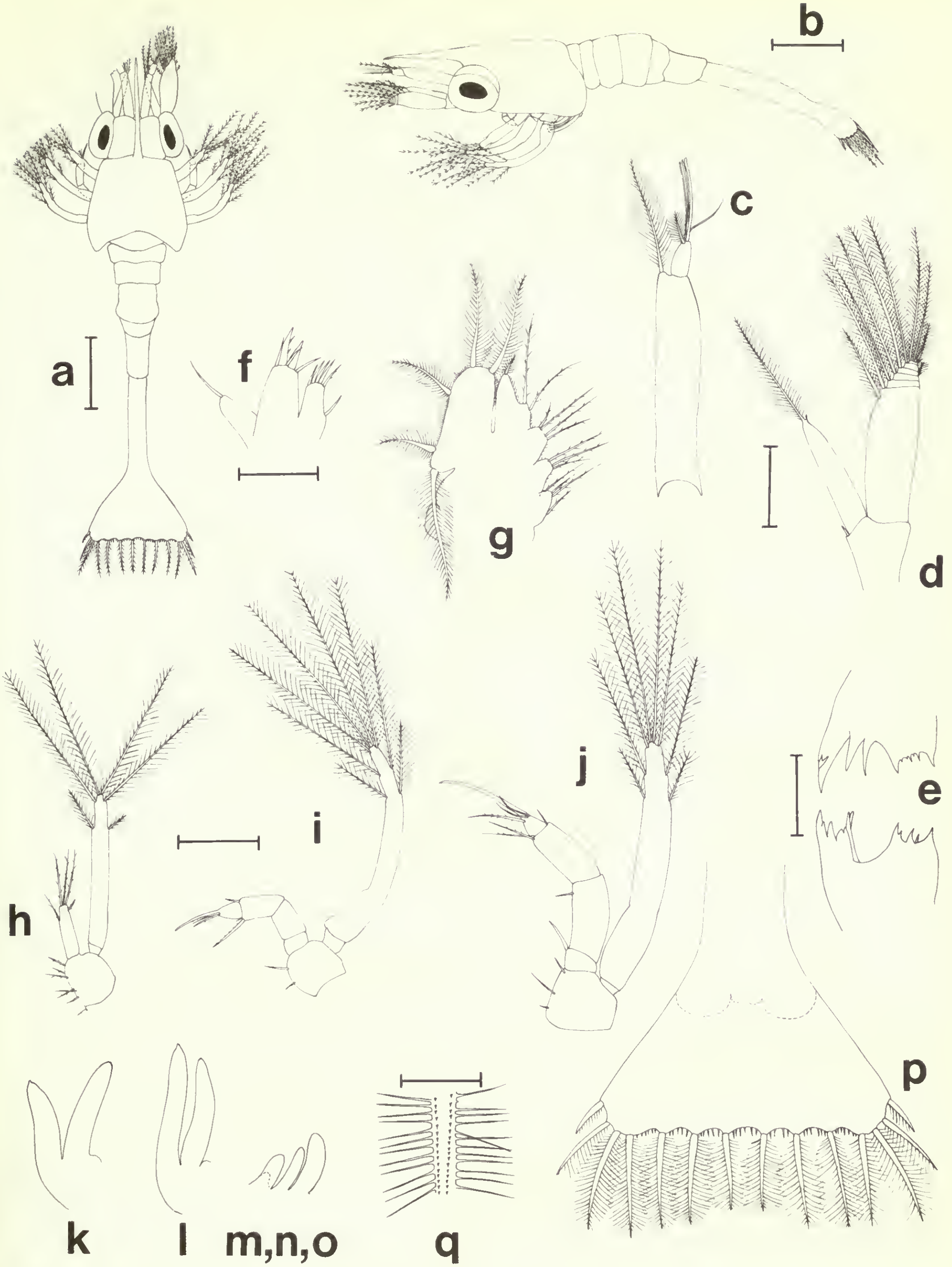


Fig. 1 Zoea 1: (a) dorsal view; (b) lateral view; (c) antenna 1; (d) antenna 2; (e) mandibles; (f) maxilla 1; (g) maxilla 2; (h) maxilliped 1; (i) maxilliped 2; (j) maxilliped 3; (k) pereiopod 1; (l) pereiopod 2; (m) pereiopod 3; (n) pereiopod 4; (o) pereiopod 5; (p) telson; (q) detail from inner pair of telsonic spines. Bar scales: a, b = 0·5 mm; c, d, h–p = 0·2 mm; f, g = 0·1 mm; e, q = 0·05 mm.

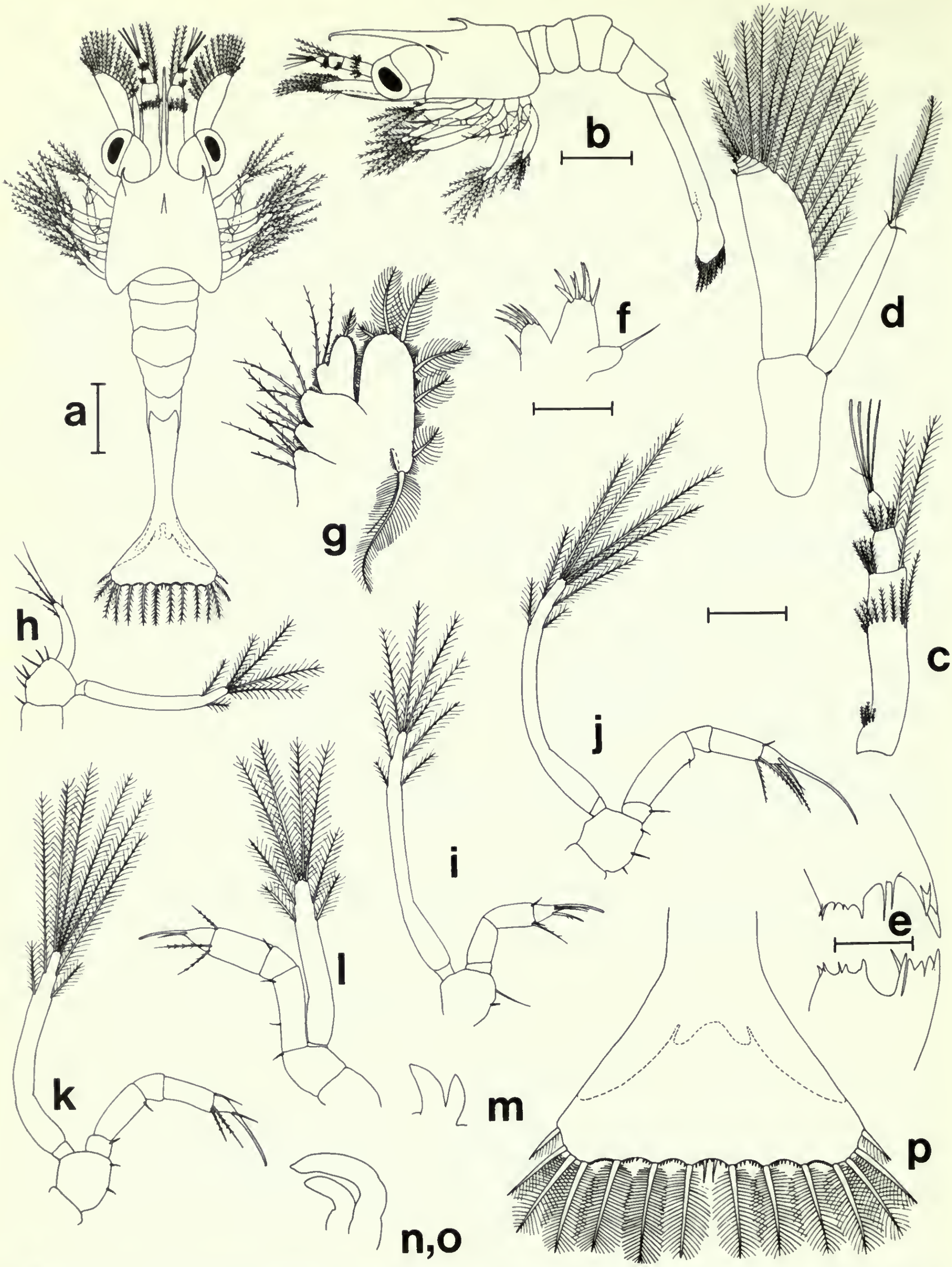


Fig. 2 Zoea 2: (a) dorsal view; (b) lateral view; (c) antenna 1; (d) antenna 2; (e) mandibles; (f) maxilla 1; (g) maxilla 2; (h) maxilliped 1; (i) maxilliped 2; (j) maxilliped 3; (k) pereiopod 1; (l) pereiopod 2; (m) pereiopod 3; (n) pereiopod 4; (o) pereiopod 5; (p) telson. Bar scales: a, b = 0·5 mm; c, d, h–p = 0·2 mm; f, g = 0·1 mm; e = 0·05 mm.

Antenna 1 (Fig. 2c): *two peduncle segments, stylocerite forming on proximal external margin of first segment; single flagellar segment with four terminal aesthetascs, two wide and two narrow.*

Antenna 2 (Fig. 2d): exopodite with distal part divided into 4 or 5 segments; wide gap between 9 distal setae and new setae added at this moult.

Pereiopods 1, 2 (Figs 2k, l): *developed, with natatory exopodite.*

Pereiopod 3 (Fig. 2m): *rudimentary, biramous.*

Pereiopods 4, 5 (Figs 2n, o): *rudimentary, uniramous.*

Abdomen (Figs 2a, b): *somite 5 with posterior margin produced into a pair of conspicuous spines, somite 6 continuous with telson.*

Telson (Fig. 2p): *developing uropods visible beneath exoskeleton* alongside telson proper; *in central group of small spines, one pair longer than others.*

ZOEA 3 (Figs 3, 4) 4·5 mm (4·2–4·7 mm)

Carapace (Fig. 3a, b): *two dorso-medial spines* and pair of small fronto-lateral spines at edge of carapace beneath eyes, former with retrorse teeth; rostrum still downturned at end to form a small hook.

Antenna 1 (Fig. 4a): *conspicuous spine medially*, stylocerite more pronounced; distal segment of peduncle bearing *first segment of internal flagellum*, single segment of *external flagellum bearing 3 wide aesthetascs distally.*

Antenna 2 (Fig. 4b): expodite with distal part divided into 3 short segments; *endopodite of 3 segments.*

Pereiopods 1, 2 (Figs 4f, g): *endopodite with internal distal margin of propodus produced slightly forward* (will become fixed finger of chela).

Pereiopod 4 (Fig. 4i): *rudimentary, uniramous.*

Pereiopod 5 (Fig. 4j): *developed, uniramous.*

Abdomen (Figs 3a, b, 4k): somites 1–5 with rudimentary pleopods, *somite 6 divided from telson by suture. Uropod endopodite with no marginal setae, exopodite with marginal setae.*

Telson (Fig. 4k): narrower but still broader distally, outer pair of spines on posterior margin considerably reduced.

ZOEA 4 (Figs 5, 6) 5·2 mm (4·7–5·5 mm)

Carapace (Figs 5a–d): *three dorso-medial spines* with retrorse teeth; *rostrum still downturned at end to form a small hook.*

Antenna 1 (Fig. 5h): rudiment of circular statocyst visible on first segment of peduncle; *single segment of external flagellum bearing 3 wide and 1 narrow aesthetascs distally.*

Antenna 2 (Fig. 5i): endopodite of 5 segments and as long or longer than the exopodite; distal part of exopodite no longer divided into short segments *but with a stout terminal tooth on outer distal edge.*

Pereiopods 1, 2 (Figs 6d, e): *endopodite with internal distal margin of propodus produced forward to about half length of dactylus* (excluding terminal setae).

Pereiopod 3 (Fig. 6f): *developed, with natatory exopodite.*

Pereiopod 4 (Fig. 6g): *developed, exopod absent or bud-like.*

Abdomen (Figs 5a, b, 6i): *uropod exopodite and endopodite both with marginal plumose setae.*

Telson (Fig. 6i): a little broader distally than proximally; spine formula as in Zoea 3 but further reduction in size of two outer pairs of spines.

ZOEA 5 (Figs 7, 8) 5·8 mm (4·8–6·1 mm)

Carapace (Figs 7a, b): *rostrum still downturned to form small hook.*

Antenna 1 (Fig. 7c): single external flagellum with 4 aesthetascs distally, *with additional group of 2 aesthetascs on internal margin.*

Antenna 2 (Fig. 7d): *endopodite of 6–8 segments*, longer than exopodite.

Pereiopods 1, 2 (Figs 8d, e): *endopodite with internal distal margin of propodus produced forward to over half length of dactylus* (excluding terminal setae).

Pereiopod 4 (Fig. 8g): *exopod absent.*

Abdomen (Fig. 7b): *pleopods on somites 1–5 rudimentary, biramous.*

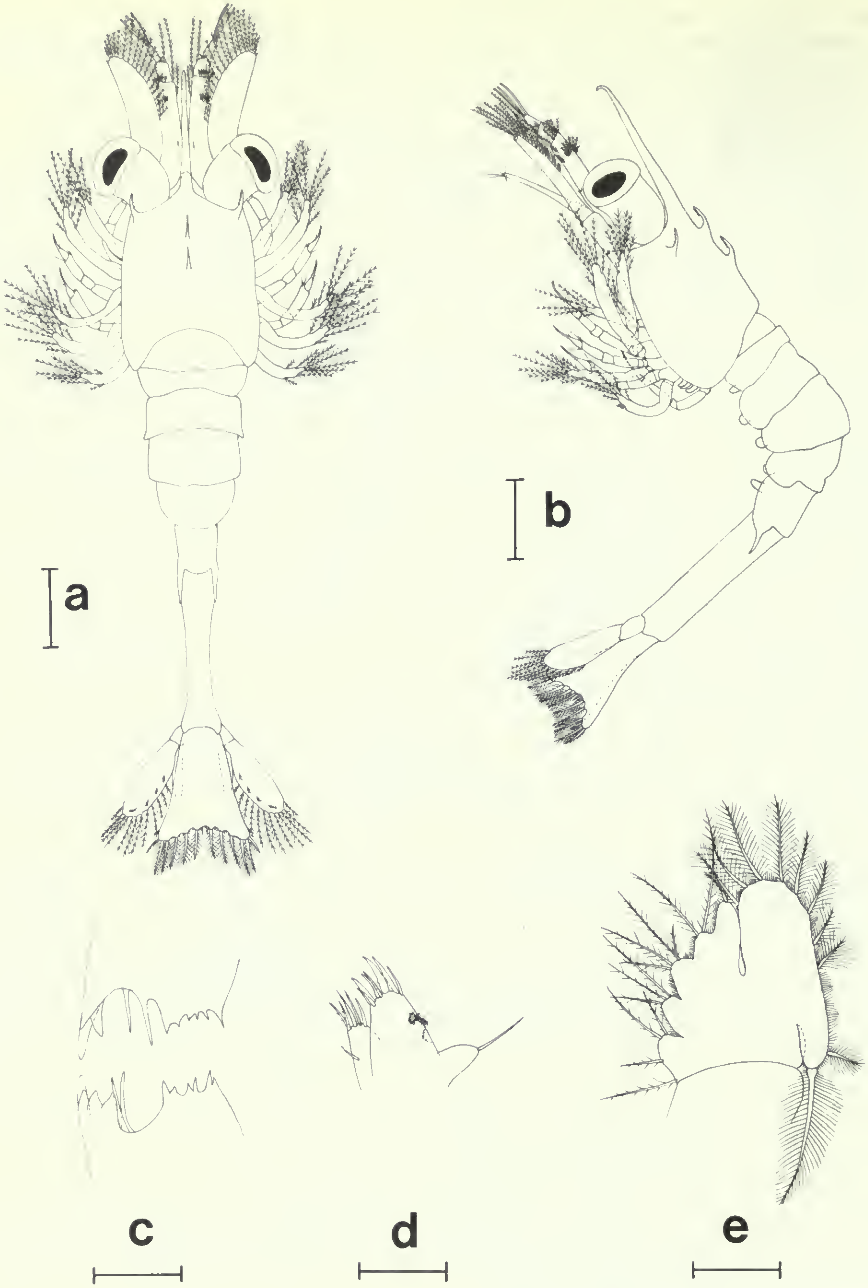


Fig. 3 Zoea 3: (a) dorsal view; (b) lateral view; (c) mandibles; (d) maxilla 1; (e) maxilla 2. Bar scales: a, b = 0·5 mm; c = 0·05 mm; d, e = 0·1 mm.

Telson (Fig. 8n): almost parallel sided; *spine formula* [*3*] *4+4* [*3*], some of small outer spines occasionally missing, posterior margin weakly concave, length about one-third overall length of telson.

ZOEA 6 (Figs 9, 10) 6·3 mm (6·1–6·6 mm)

Carapace (Fig. 9a): *short plumose seta in angle of anterior dorso-medial spine, rostrum still downturned to form small hook.*

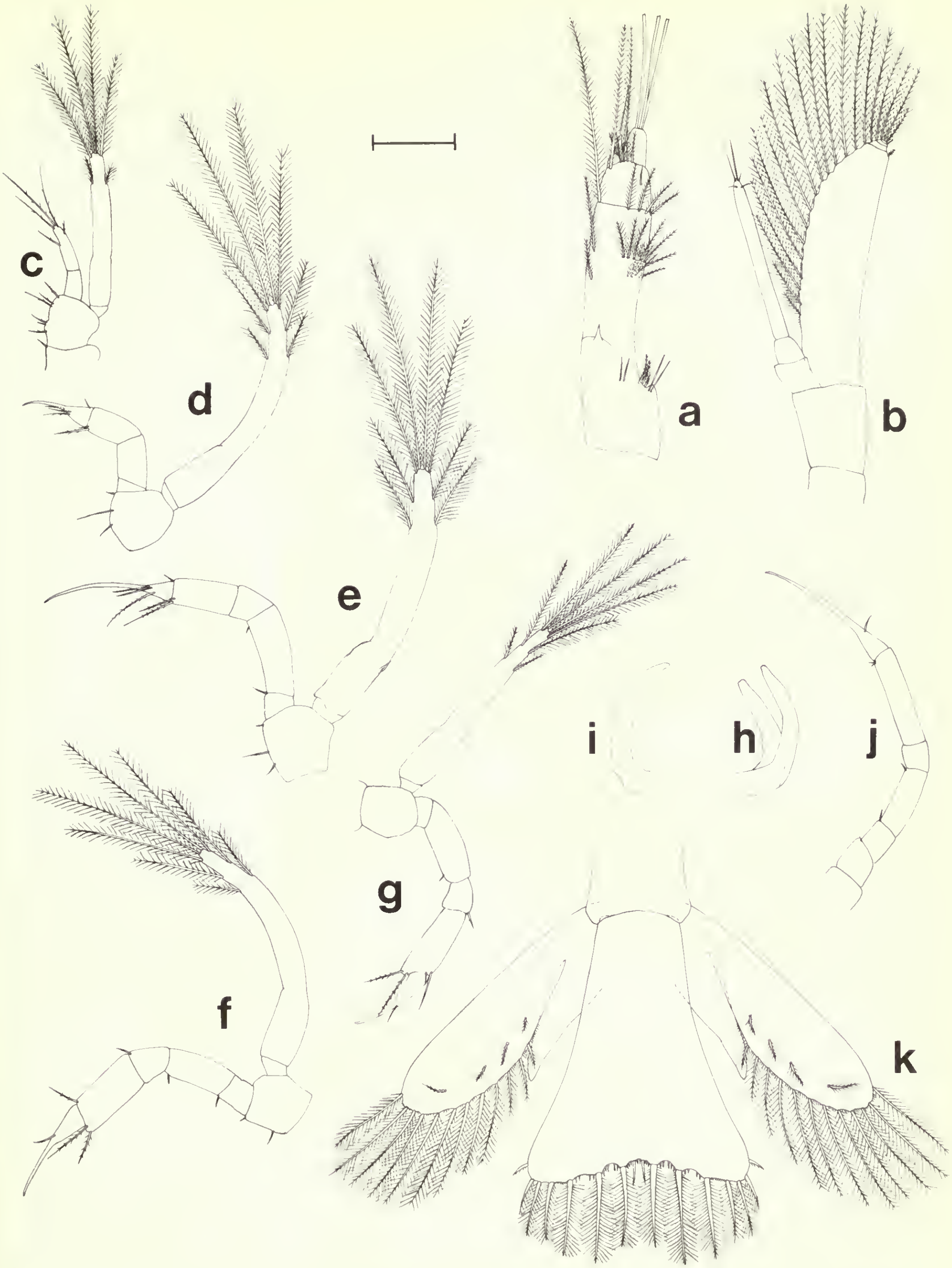


Fig. 4 Zoea 3: (a) antenna 1; (b) antenna 2; (c) maxilliped 1; (d) maxilliped 2; (e) maxilliped 3; (f) pereiopod 1; (g) pereiopod 2; (h) pereiopod 3; (i) pereiopod 4; (j) pereiopod 5; (k) telson. Bar scale = 0·2 mm.

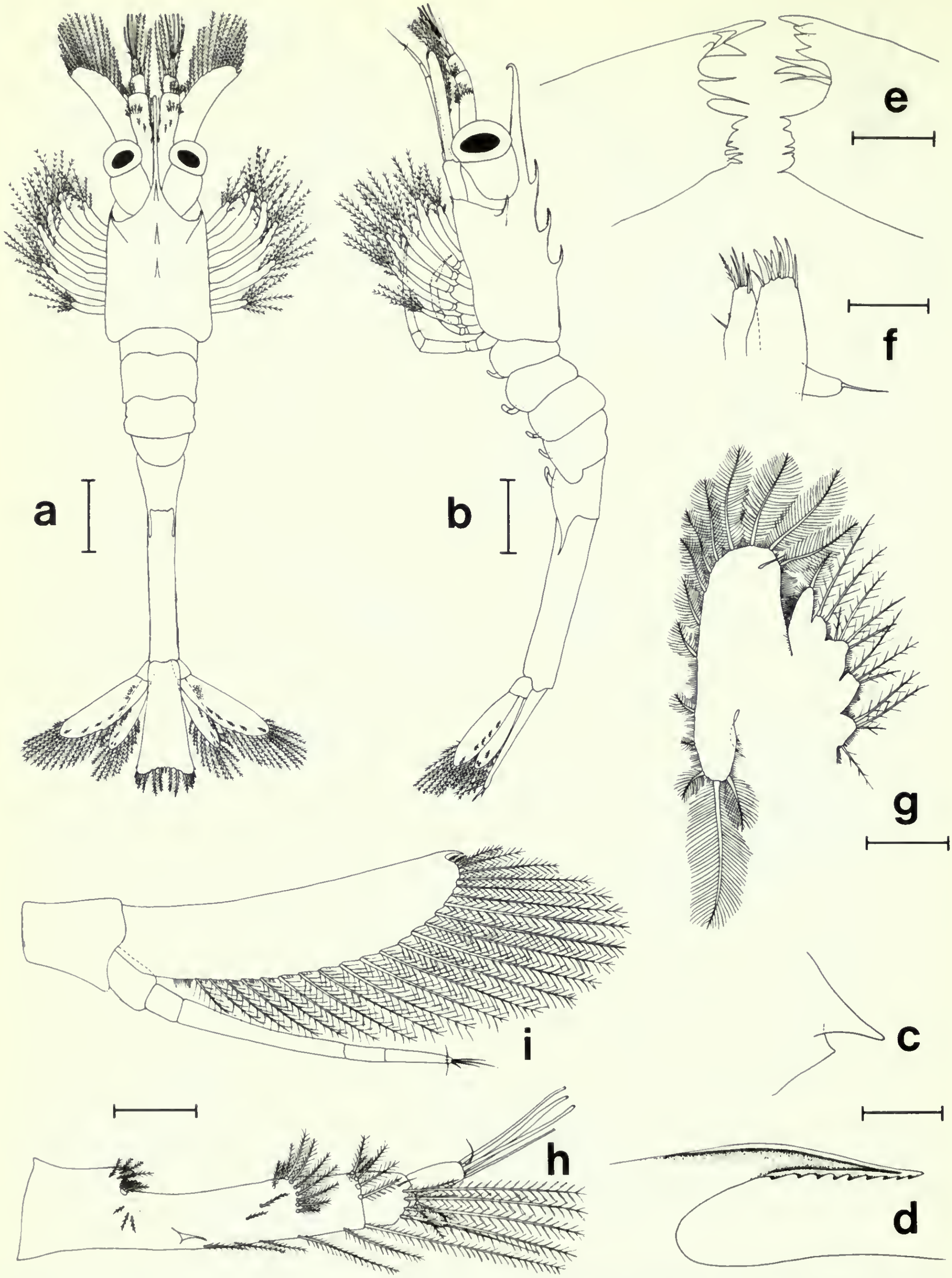


Fig. 5 Zoea 4: (a) dorsal view; (b) lateral view; (c) antero-lateral teeth of carapace; (d) first dorsomedial carapace spine; (e) mandibles; (f) maxilla 1; (g) maxilla 2; (h) antenna 1; (i) antenna 2. Bar scales: a, b = 0·5 mm; c–e = 0·05 mm; f, g = 0·1 mm; h, i = 0·2 mm.

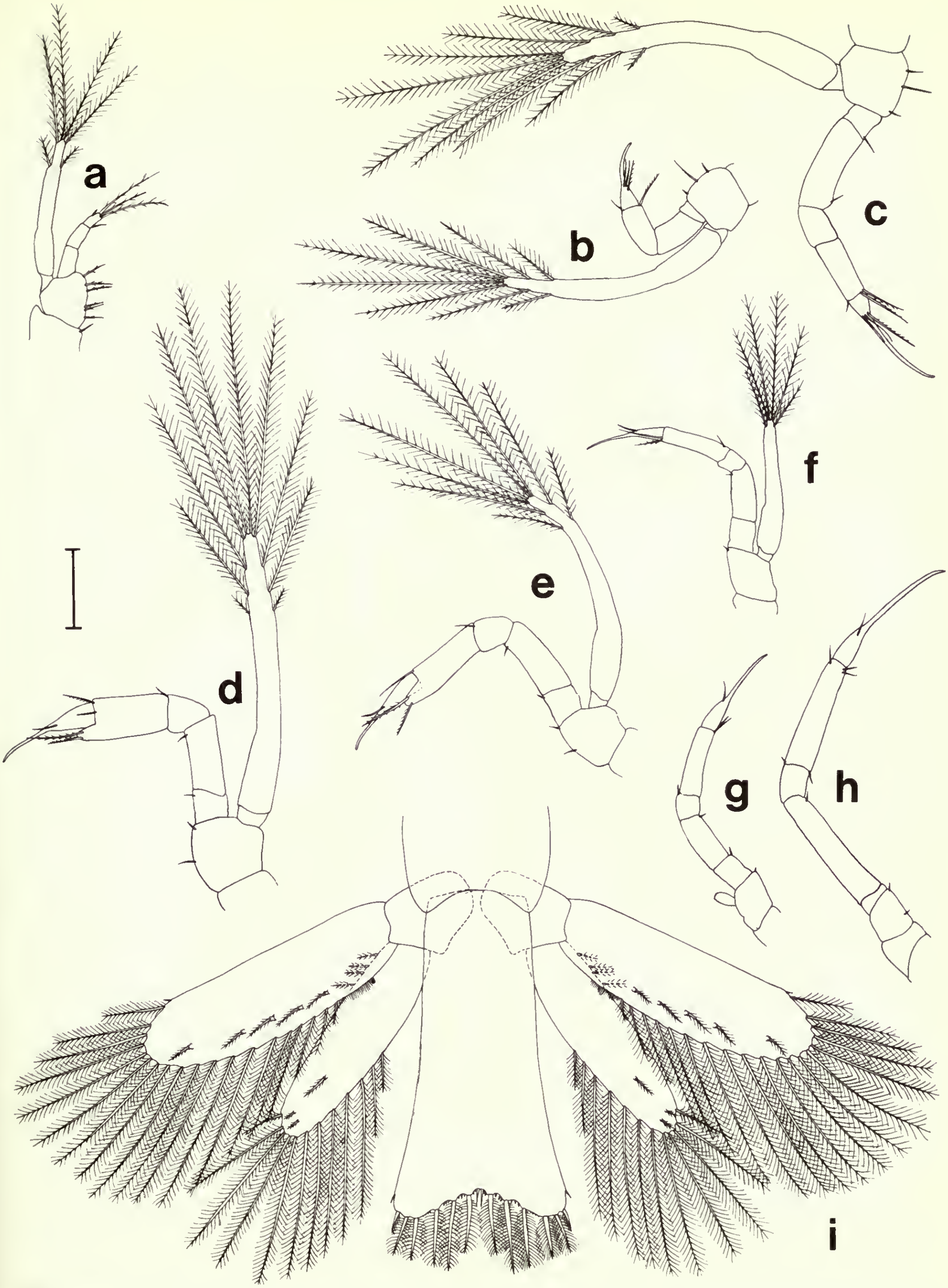


Fig. 6 Zoea 4: (a) maxilliped 1; (b) maxilliped 2; (c) maxilliped 3; (d) pereiopod 1; (e) pereiopod 2; (f) pereiopod 3; (g) pereiopod 4; (h) pereiopod 5; (i) telson. Bar scale = 0·2 mm.

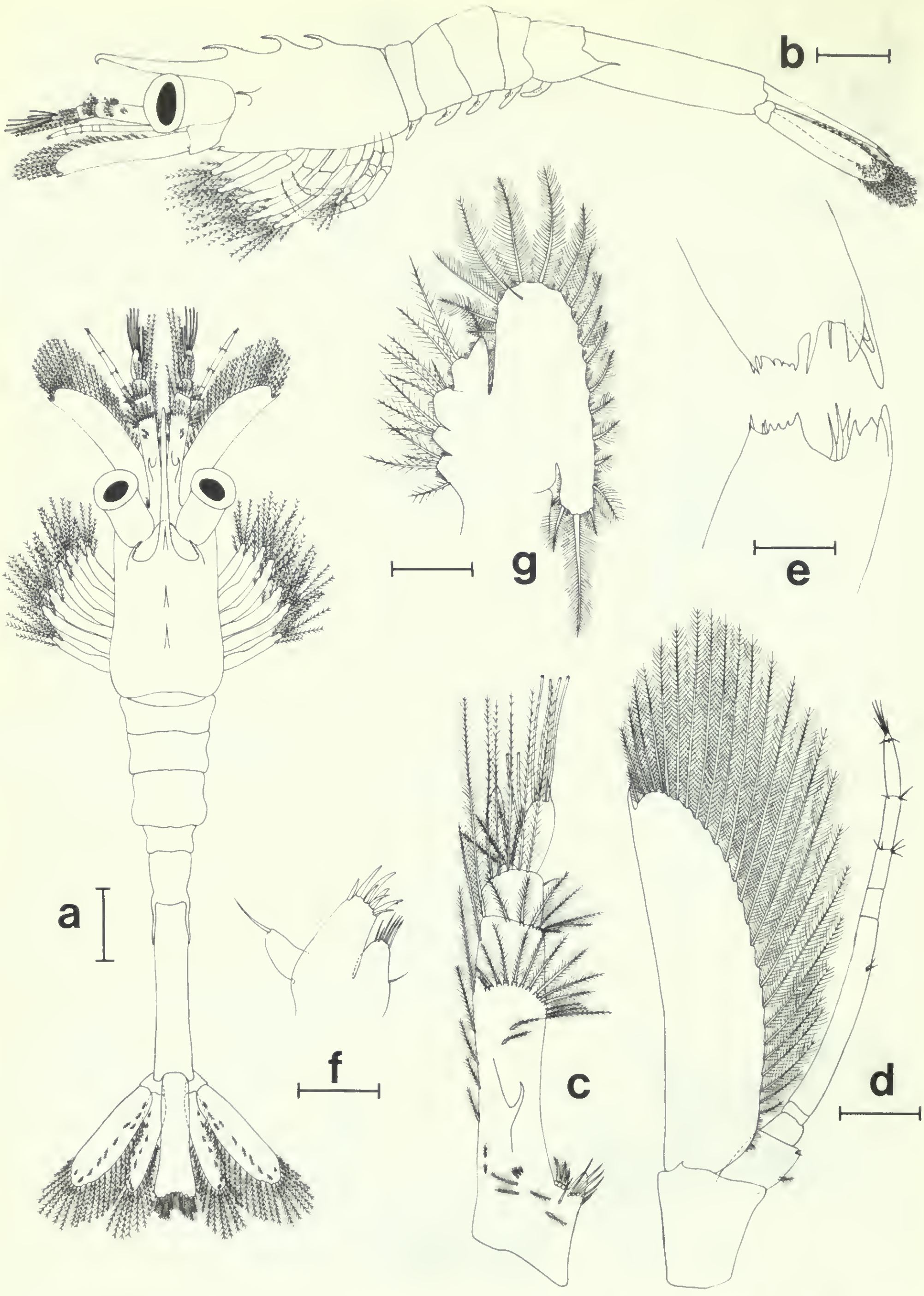


Fig. 7 Zoea 5: (a) dorsal view; (b) lateral view; (c) antenna 1; (d) antenna 2; (e) mandibles; (f) maxilla 1; (g) maxilla 2. Bar scales: a, b = 0·5 mm; c, d = 0·2 mm; e = 0·05 mm; f, g = 0·1 mm.

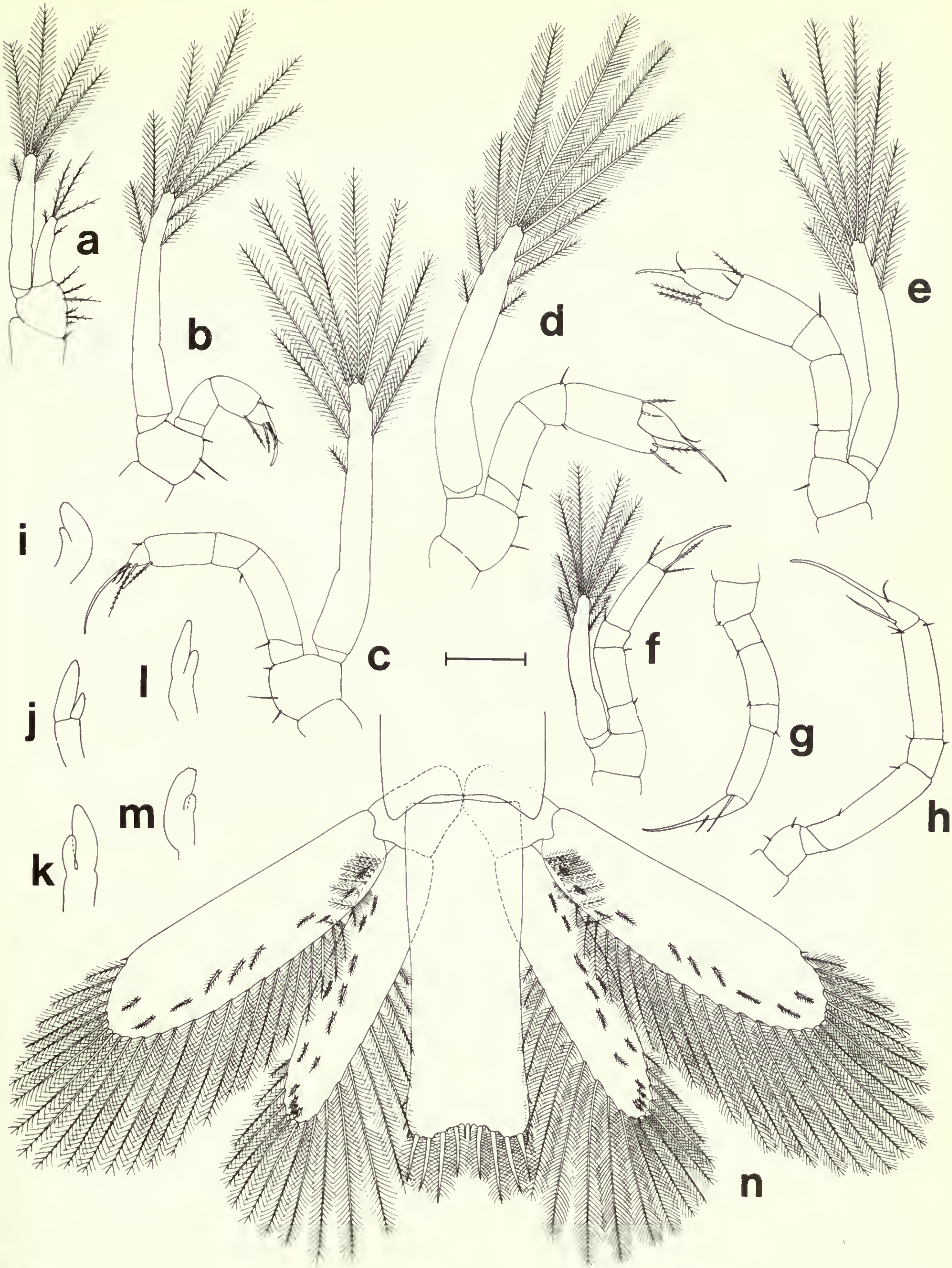


Fig. 8 Zoea 5: (a) maxilliped 1; (b) maxilliped 2; (c) maxilliped 3; (d) pereiopod 1; (e) pereiopod 2; (f) pereiopod 3; (g) pereiopod 4; (h) pereiopod 5; (i) pleopod 1; (j) pleopod 2; (k) pleopod 3; (l) pleopod 4; (m) pleopod 5; (n) telson. Bar scale = 0·2 mm.

Antenna 1 (Fig. 9c): internal flagellum of two segments.

Antenna 2 (Fig. 9d): *endopodite of at least 9 segments.*

Maxilliped 1 (Fig. 10a): *exopodite with 3* (usually) *proximo-lateral plumose setae.*

Pereiopods 1, 2 (Figs 10d, e): *endopodite with immovable finger of propodus produced forward to almost length of dactylus* (excluding terminal setae).

Abdomen (Figs 9b, 10i–m): *pleopods with rudimentary setae on margins of endopodite and exopodite*, endopodite of pleopods 2–5 with rudimentary appendix interna.

Telson (Fig. 10n): *narrowing distally*, posterior margin weakly convex and *length just over a quarter overall length of telson; small spines between large spines reduced in number to a central pair.*

ZOEA 7 (Figs 11–13) 6·5 mm (6·3–6·8 mm)

A few specimens have already metamorphosed to post larvae at this moult. Meristic characters from these post larvae have not been included in Table 1 nor in the following description.

Carapace (Fig. 11a): rostrum with weak distal hook or straight, occasionally a single ventral tooth.

Antenna 1 (Fig. 12a): *internal flagellum of 3 segments, external flagellum of 2 segments.*

Antenna 2 (Fig. 12b): *endopodite of at least 12 segments.*

Maxilliped 1 (Fig. 12f): exopodite with 5 (usually) proximo-lateral plumose setae.

Pereiopods 1, 2 (Figs 13a, b): *propodus 'palm' almost as wide as long* (0·8 : 1).

Telson (Fig. 13k): *no small spines between large spines.*

POST LARVA 1 (Figs 14–17) 6·7 mm (6·3–7·1)

More than 50% of specimens have metamorphosed to post larvae at this moult. Meristic characters from the post larvae only have been included in Table 1.

Carapace (Figs 14a, b, 15b): *rostrum usually with 6 dorsal and 2 ventral teeth*, rostral tip straight (see intermediate condition of rostrum Fig. 15a) *supraorbital spines missing.*

Antenna 1 (Fig. 15c): internal flagellum of 6–9 segments and external flagellum of 6 segments, *distal group of aesthetascs reduced to three.*

Antenna 2 (Fig. 15d): endopodite multisegmented, several times longer than the scaphocerite.

Mandible (Figs 16a, b): *divided into pars incisiva and pars molaris*, lacinia mobilis no longer present and palp (three-jointed in adult) not yet appeared.

Maxilla (Fig. 16c): up to 16 setae on basal endite.

Maxilla 2 (Fig. 16d): *complete loss of setae on coxal endite and a reduction to 1 seta on endopodite*, increases in setae on basal endites.

Maxilliped 1 (Fig. 15e): large increase in setae on internal margin of basis (zoea 7: 7–8, post larva 1: 27–30).

Maxilliped 2 (Fig. 15f): endopodite with dactylus, propodus and merus flattened, *exopodite shortened and with reduced plumose setae.*

Maxilliped 3 (Fig. 15g): endopodite dactylus shortened, *exopodite reduced* to less than half the length of endopodite.

Pereiopods 1, 2 (Figs 16e, f): ischium, merus and carpus lengthened, *exopodite reduced* to less than length of ischium of endopodite, plumose setae much reduced.

Pereiopod 3 (Fig. 16g): endopodite dactylus tapering evenly distally, other joints lengthened, *exopodite reduced*, extending less than halfway along ischium of endopodite, plumose setae much reduced.

Pereiopods 4, 5 (Figs 16h, i): endopodite dactylus tapering evenly distally, other joints lengthened.

Pleopod 1 (Fig. 17a): *ratio of endopodite to exopodite 1 : 3·5*, endopodite bearing terminal plumose setae, exopodite fringed with long plumose setae.

Pleopods 2–5 (Figs 17b–e): endopodite over half length of exopodite, both with long, marginal plumose setae, endopodite with appendix interna bearing well-developed intero-distal coupling hooks.

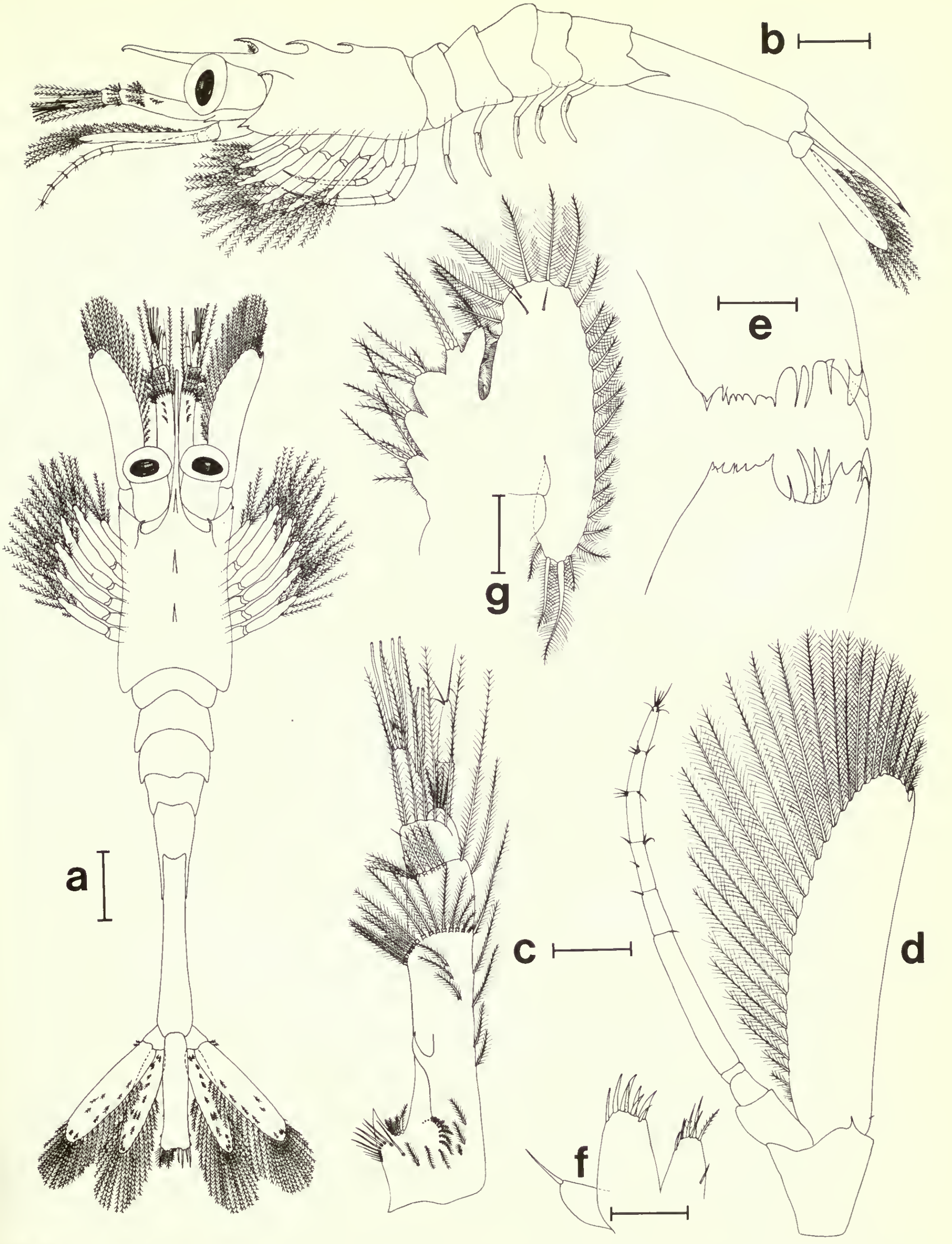


Fig. 9 Zoea 6: (a) dorsal view; (b) lateral view; (c) antenna 1; (d) antenna 2; (e) mandibles; (f) maxilla 1; (g) maxilla 2. Bar scales: a, b = 0·5 mm; c, d = 0·2 mm; e = 0·05 mm; f, g = 0·1 mm.

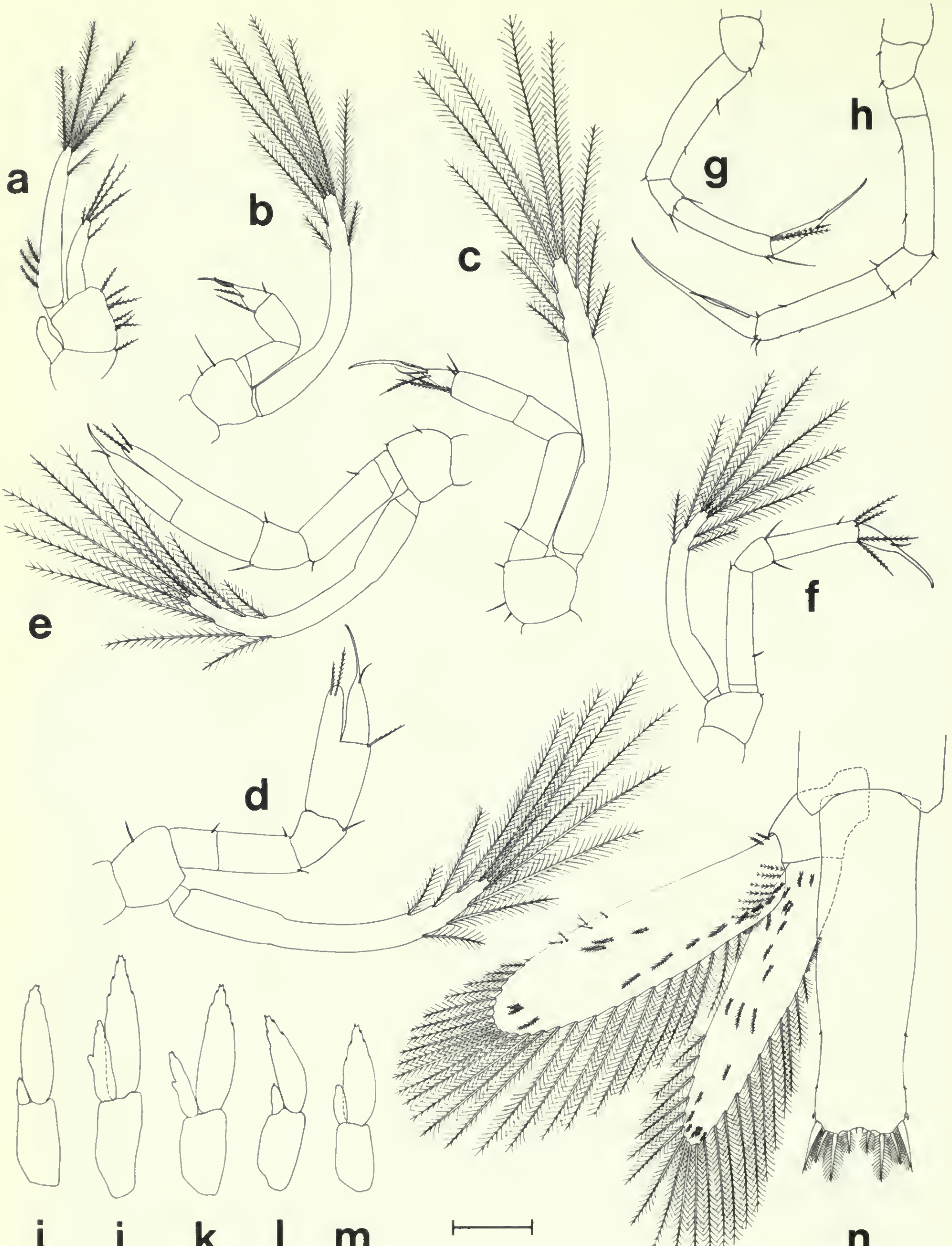


Fig. 10 Zoea 6: (a) maxilliped 1; (b) maxilliped 2; (c) maxilliped 3; (d) pereiopod 1; (e)pereiopod 2; (f) pereiopod 3; (g) pereiopod 4; (h) pereiopod 5; (i) pleopod 1; (j) pleopod 2; (k) pleopod 3; (l) pleopod 4; (m) pleopod 5; (n) telson. Bar scale = 0·2 mm.

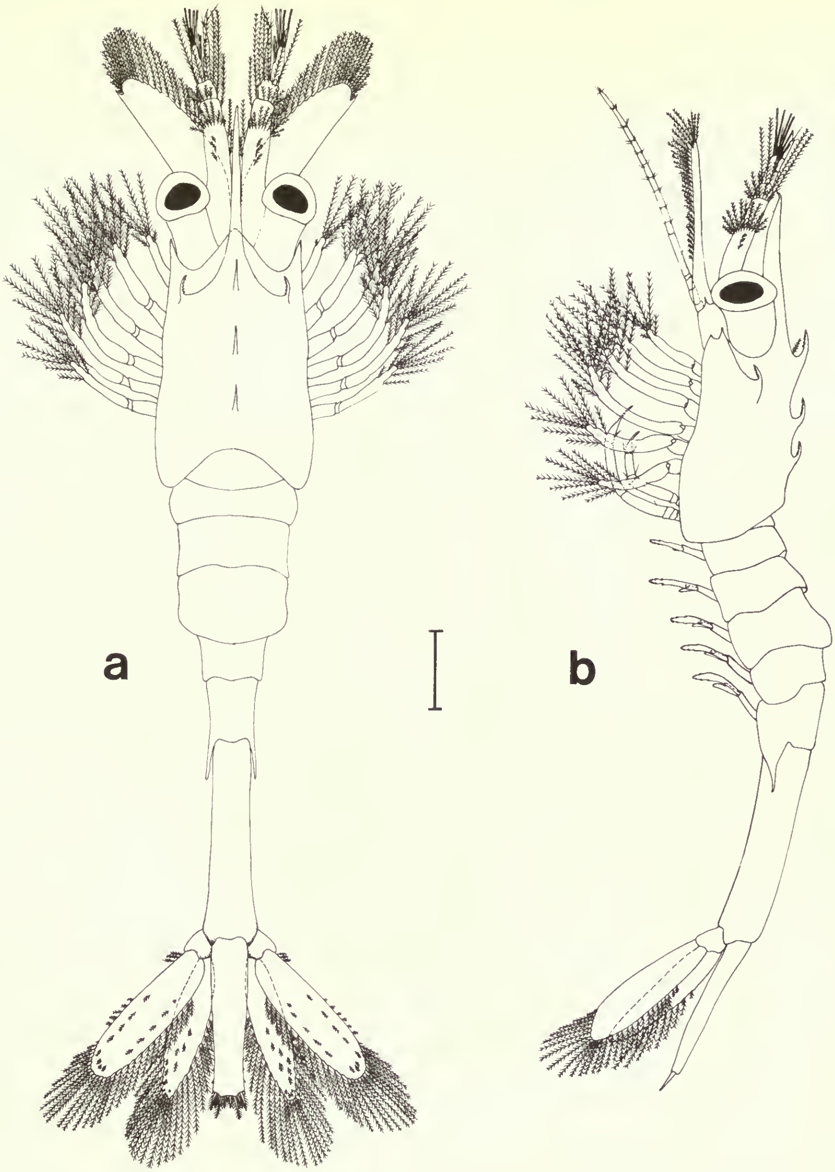


Fig. 11 Zoea 7: (a) dorsal view; (b) lateral view. Bar scale = 0·5 mm.

Abdomen (Fig. 14b): *fifth abdominal somite truncated*, point of stages 2–7 much reduced.

Telson (Fig. 17f): *extremely narrow, posterior margin tapering to a point* and bearing a pair of small (outer) and large (inner) spines and medially a pair of plumose setae. Two pairs of stout spines developed on lateral margins of telson (see intermediate condition found in specimens with intermediate rostral form Fig. 17g).

Effect of antibiotic

The effect of antibiotic on the length of intermoult period on two series each of 108 larvae kept at 18 °C is shown in Fig. 17a. Larvae reared without antibiotic (−AB) moult in less than 5 days to stage 3 compared with larvae reared with antibiotic (+AB) which take an average of

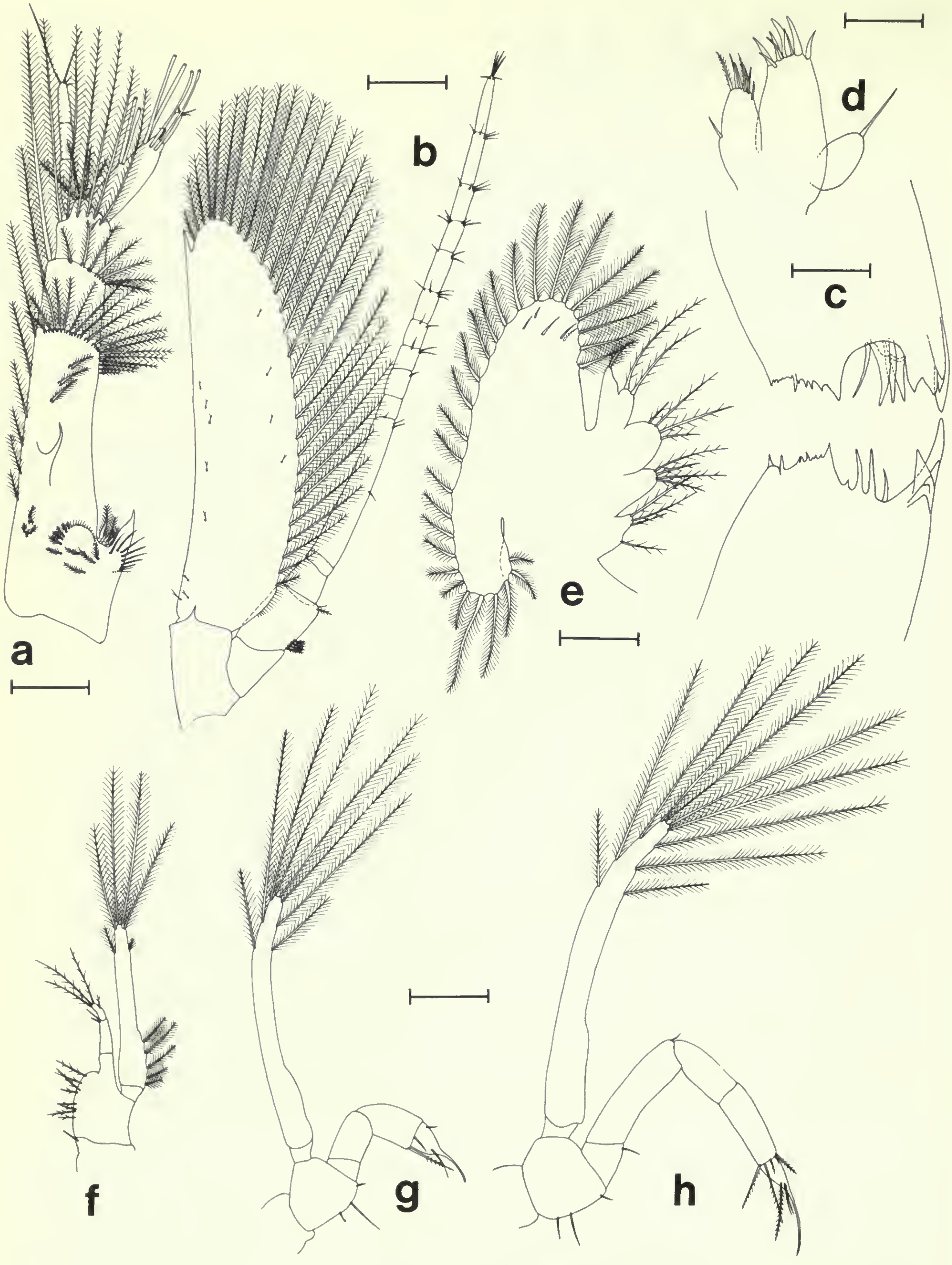


Fig. 12 Zoea 7: (a) antenna 1; (b) antenna 2; (c) mandibles; (d) maxilla 1; (e) maxilla 2; (f) maxilliped 1; (g) maxilliped 2; (h) maxilliped 3. Bar scales: a, b, f–h = 0·2 mm; c = 0·05 mm; d, e = 0·1 mm.

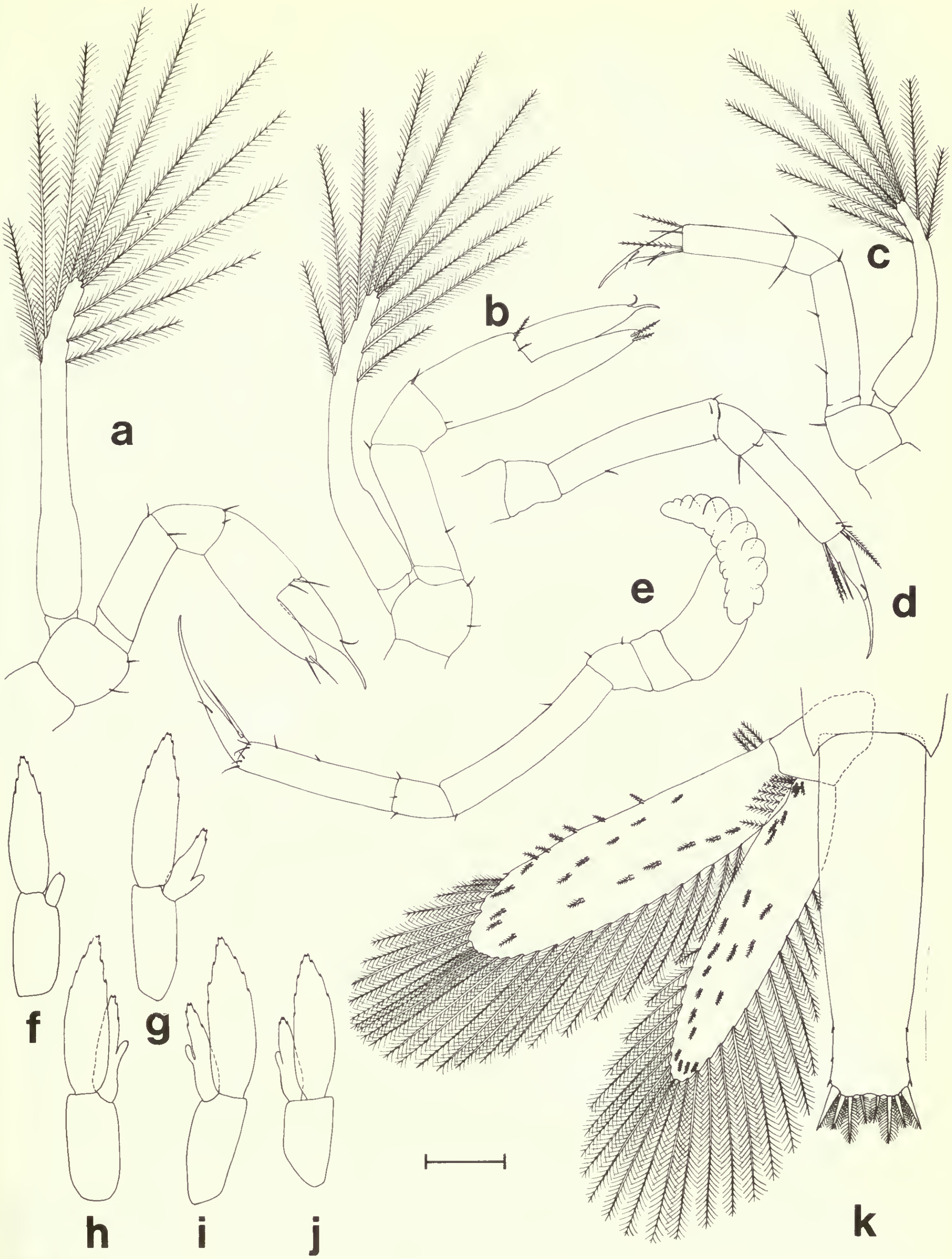


Fig. 13 Zoea 7: (a) pereiopod 1; (b) pereiopod 2; (c) pereiopod 3; (d) pereiopod 4; (e) pereiopod 5; (f) pleopod 1; (g) pleopod 2; (h) pleopod 3; (i) pleopod 4; (j) pleopod 5; (k) telson. Bar scale = 0·2 mm.

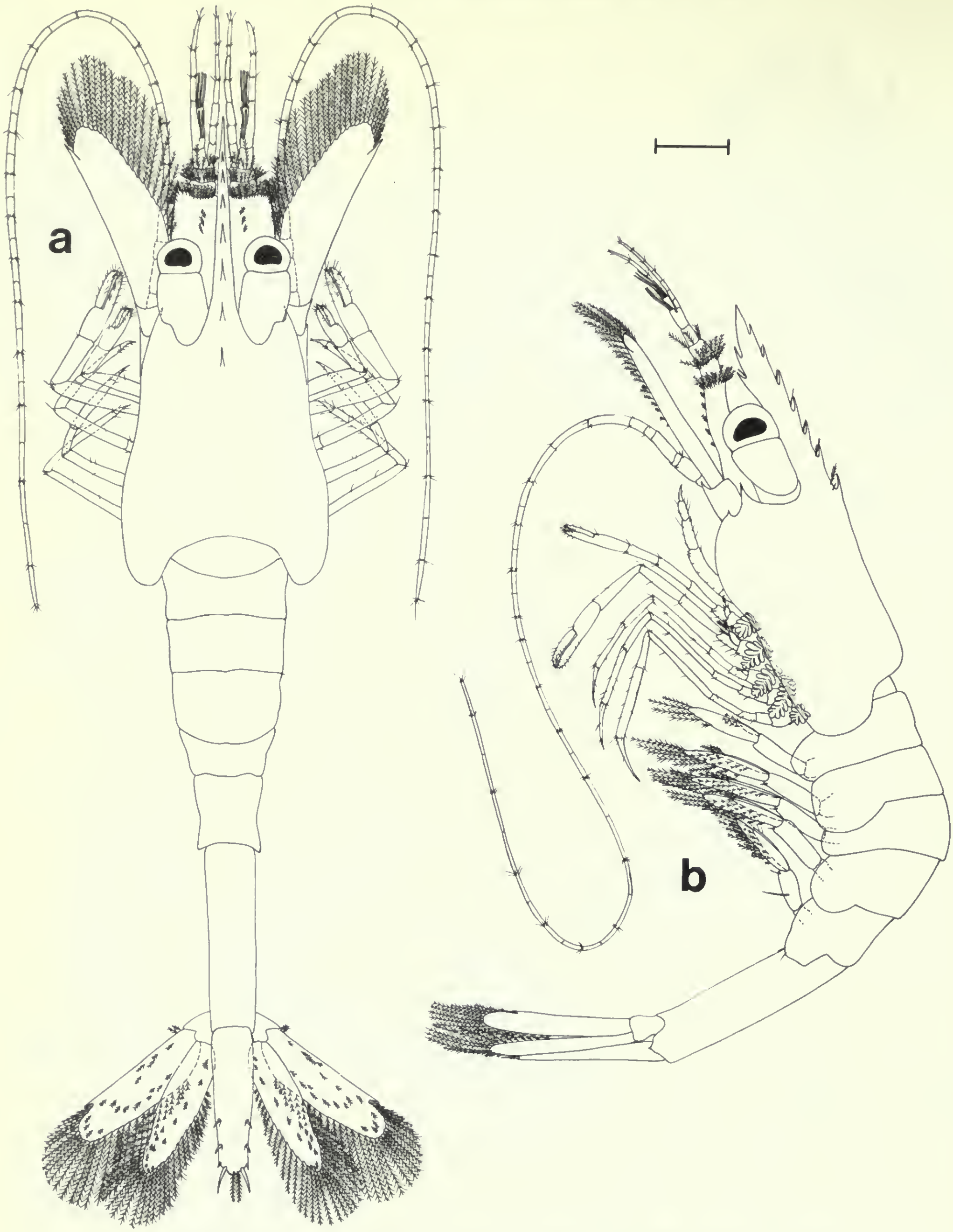


Fig. 14 Post larva 1: (a) dorsal view; (b) lateral view. Bar scale = 0·5 mm.

nearly 7 days. This advantage is maintained throughout the remaining period of larval development. Post larval stage is reached by at least 50% of −AB larvae at moult 7–8; metamorphosis is delayed until moult 9–10 in +AB larvae.

Fig. 17b shows the growth of the two series of larvae. Faster growth is shown by +AB larvae until stage 4 when −AB larvae overtake them in size. This increase is maintained throughout larval development with the two series coming close at moult 8. From this moult the difference in growth widens markedly, −AB larvae further increasing their average size over +AB larvae.

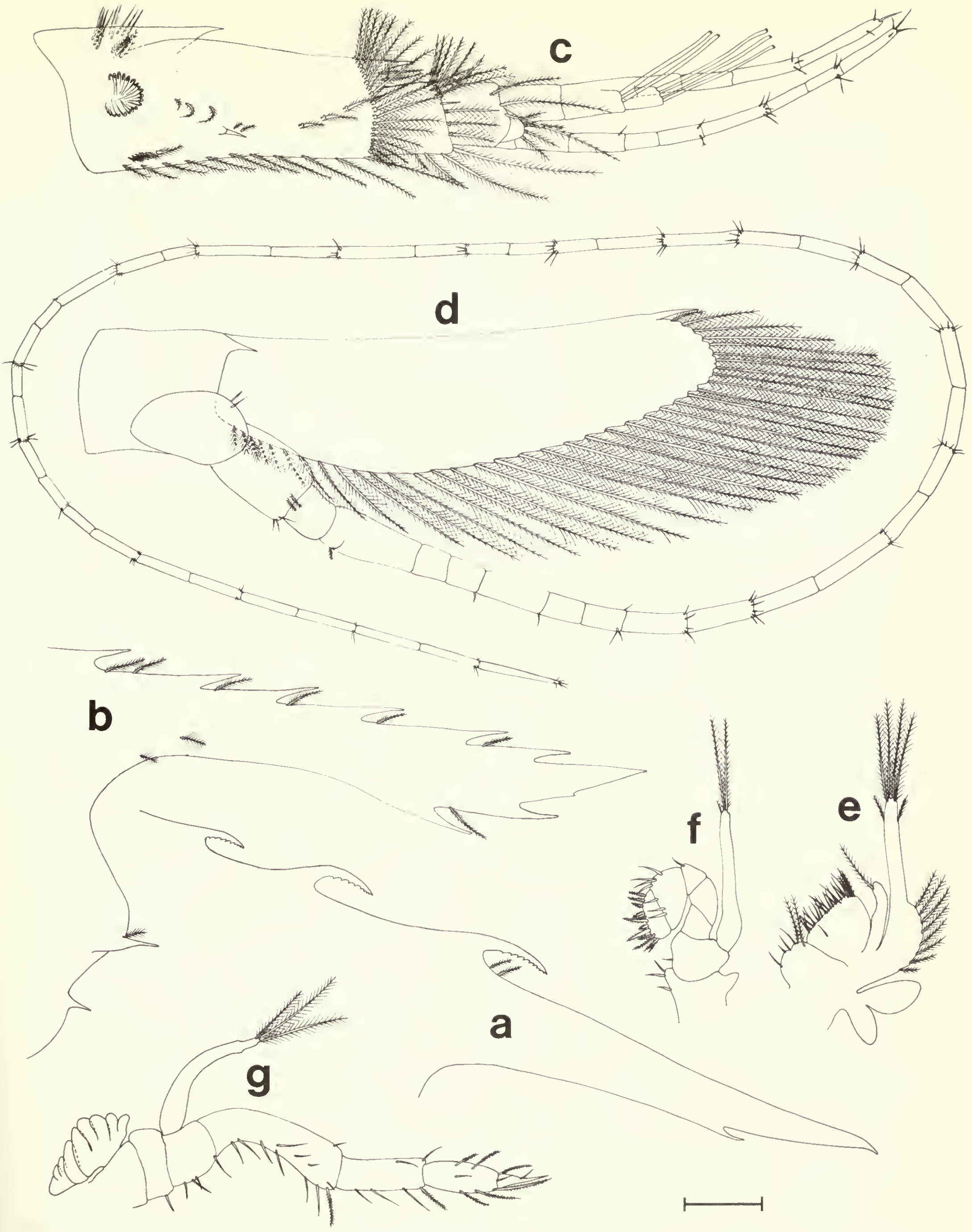


Fig. 15 Intermediate stage: (a) rostrum. Post larva 1: (b) rostrum; (c) antenna 1; (d) antenna 2; (e) maxilliped 1; (f) maxilliped 2; (g) maxilliped 3. Bar scale = 0·2 mm.

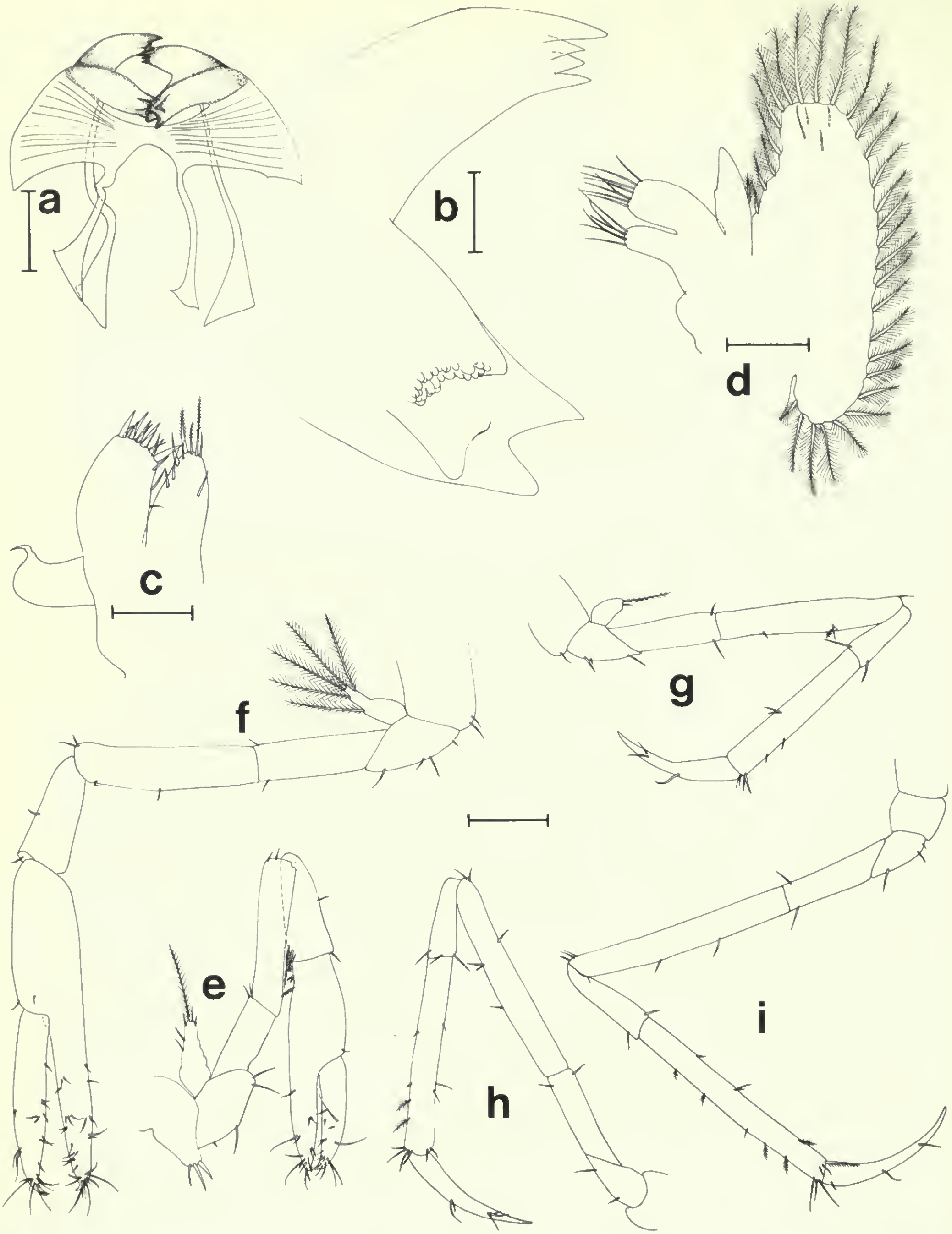


Fig. 16 Post larva 1: (a) mandibles and musculature; (b) mandible with *pars incisiva* (above) and *pars molaris* (below); (c) maxilla 1; (d) maxilla 2; (e) pereiopod 1: (f) pereiopod 2; (g) pereiopod 3; (h) pereiopod 4; (i) pereiopod 5. a, e–i = 0·2 mm; c, d = 0·1 mm; b = 0·05 mm.

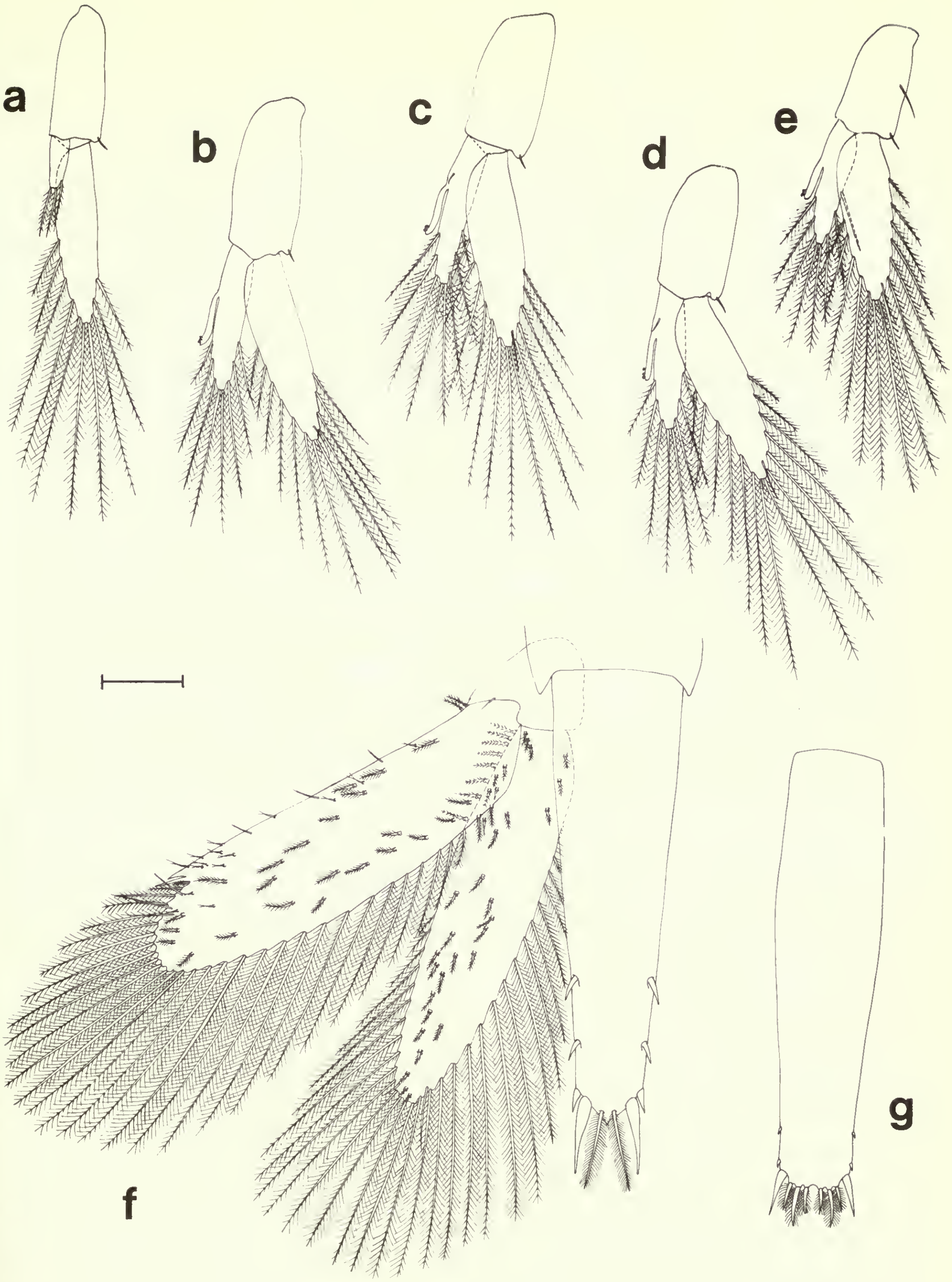


Fig. 17. Post larva 1: (a) pleopod 1; (b) pleopod 2; (c) pleopod 3; (d) pleopod 4; (e) pleopod 5; (f) telson. Intermediate stage: (g) telson. Bar scale = 0·2 mm.

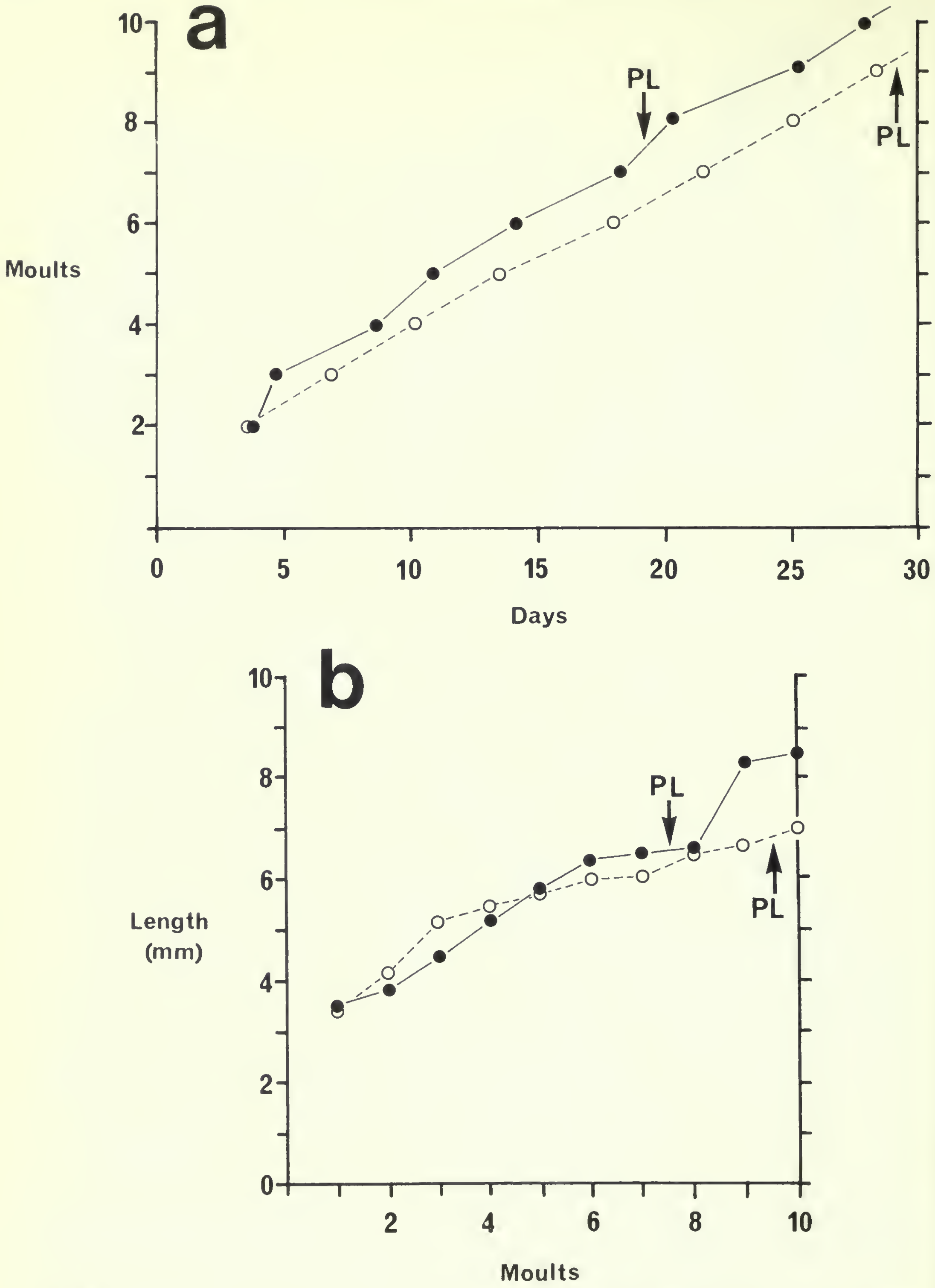


Fig. 18 Effect on (a) intermoult period, (b) growth rate of larvae reared with (○ - - - - - ○) and without (●—— ●) antibiotic. Figures averaged from 10 individuals at each stage.

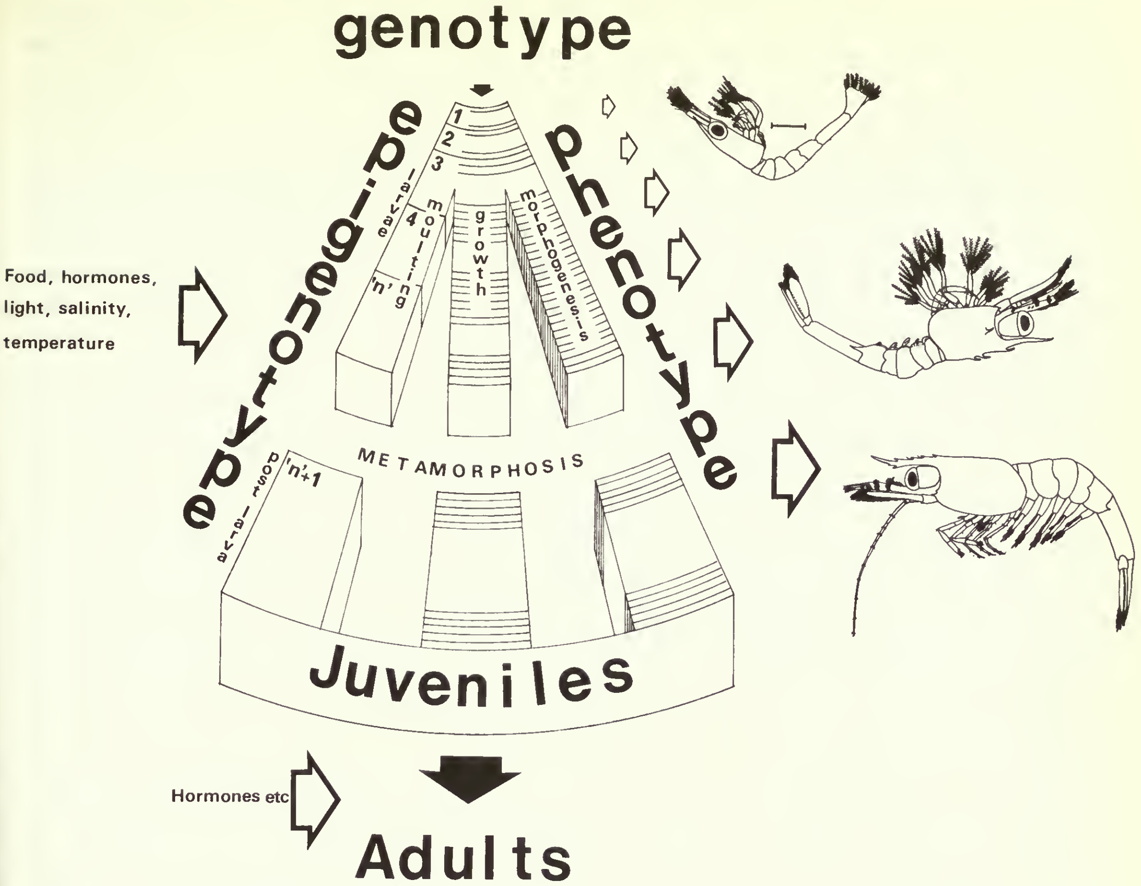


Fig. 19 Larval development of decapod Natantia showing the relationship between genetic input, epigenesis and the internal and external environmental factors which affect the semi-independent developmental processes of moulting, growth and morphogenesis. This results in larval phenotpyic variation in morphometric and meristic characters and in the number of stages. The system stabilizes in the post larva after metamorphosis. Bar scale = 0·5 mm.

Discussion

Effect of antibiotic on morphogenesis

The results of detailed comparisons of moults and larvae at each stage from specimens reared with (+AB) and without (−AB) antibiotic are shown in Table 1. There was no appreciable effect on normal phenotypic variation. However, there was a noticeable effect on the average intermoult period, which in −AB larvae was 2·9 days while in +AB larvae it was 3·5 days (Fig. 18a). This is the reverse of the situation in the brachyuran *Hyas araneus* (Linnaeus) in which the intermoult period was shortened at both 10 and 15 °C at the same concentration of antibiotics used in the present work (Christiansen, 1971). Christiansen also found that mortality of laboratory reared larvae was lower when antibiotics were used. This effect was not found in *Palaemon* (*Palaemon*) *longirostris;* 92% survival was recorded in −AB larvae but only 71% in +AB larvae. In two experiments made with two replicate populations of 100 and 25 larvae of *Palaemon serratus*, Wickins (1972) found that stocking densities did affect total percentage survival but that the addition of antibiotics had little effect on survival (100 larvae/litre: −AB 59% survival, +AB 58%; 25 larvae/litre: −AB 88%, +AB 86% from Wickins, 1972). The moult to post larvae in *P.* (*P.*) *longirostris* in the present work was delayed by about 10 days after two further moults had occurred in +AB larvae. Wickins also found that during the first 5–7 days of metamorphosis in each trial, more (average 28%) larvae had metamorphosed at any given time in the cultures without antibiotics. It was considered that either the presence of antibiotics or their bactericidal action was responsible for retarding the development of the larvae.

In the present work it was found that the effect of antibiotics on growth changed during the course of larval development (Fig. 18b). The initial increase in size by +AB larvae over −AB larvae may be a direct result of bacterial infection in the cultures. In the open sea the numbers of bacteria are low and it seems likely that this is correlated with a lack of solid surfaces on which to settle (Walne, 1958). In the compartmented rearing trays used in this study there is a high surface to volume ratio and bacteria are introduced into the trays both on the larvae themselves and on the *Artemia* nauplii used as food. It seems likely, therefore, that the unnatural stress introduced by the build-up of bacteria is successfully counteracted initially by the use of antibiotics and actually enhances growth compared with the −AB larvae. That this increased growth is not maintained may be due to a number of factors but one which might repay further investigation would be an assessment of the effect on the populations of gut flora. This would adversely affect food absorption and consequently growth. At the eighth moult both the +AB and −AB larvae are similar in size. This apparent slowing of growth in −AB larvae occurs after the majority of specimens have moulted to post larvae. Much internal reorganization takes place in connection with the change in the swimming mode. The upside down, tail first, thoracic exopodite swimming and planktonic mode of life is replaced by a basically benthic mode, and when swimming occurs the post larva is the right way up, head first and uses abdominal pleopods. The internal changes have been monitored by Campillo *et al.* (1975) who found that during larval development the growth process in *Palaemon serratus* (Pennant) alternates between periods of hyperplasy (stages 1–4, 5–7) and hypertrophy (stages 4–5, 7 to post larva). Prior to the post larval moult any growth is by an increase in cell size rather than from an increase in cell number. Regnault (1971) found that free amino acids had two peaks during the larval development of *Crangon septemspinosa* Say at stage 3 and last larval stage. These biochemical and cellular changes tie in with two major periods of morphogenesis, i.e. the development of uropods and the loss of the thoracic swimming exopods and their replacement with abdominal swimming pleopods. Morphogenesis of the mouthparts (compare Figs 12c, d, e and 16a, b, c, d), necessitated by the change in diet, accompany these other changes in the mode of propulsion at the post larval moult. Hence at this moult there is unlikely to be much spare energy for growth. Once this first post larval moult is passed, growth rate increases and is faster in these −AB individuals than at any time during the development of either +AB or −AB larvae.

The process of development

Moulting, growth and morphogenesis in the early stages of natant development are synchronous. For the first few moults phenotypic variation is small or even absent, for example the number of plumose setae on the exopodite of antenna 2 in zoea 1 is 9, while in maxilla 2 the figures are 5 and 7 for zoeae 1 and 2 respectively (Table 1). Both size and morphology of these early stages are largely predictable. However, in later larval development there is some independence of the three development processes (Fig. 19). This results in variable numbers of stages and larvae of intermediate stage morphology in both plankton and laboratory reared material. This variability has been recorded in the Palaemonidae by Faxon (1879), Gurney (1924*a*), Gurney & Lebour (1941), Broad (1957*a*), Tsurnamal (1963), Little (1969) and Fincham (1977, 1979).

Knowlton (1974) in his hierarchical representation of energy flow in caridean larval development gives high priority to general maintenance and survival, moulting is placed next followed by the synthetic processes of growth, morphogenesis and regeneration which are given equal weight. The genetic content of the fertilized egg is fixed and the embryos and larvae develop through a series of 'causal relations' (Waddington, 1953). This epigenesis may be influenced by a number of factors including food (Broad, 1957*b*; Reeve, 1969; Knowlton, 1974), hormones (Hubschman, 1963; Costlow, 1968; Little, 1969), light (Knowlton, 1974), salinity and temperature (Sandifer, 1973; Knowlton, 1974). The virtual independence of the development processes is shown diagrammatically in Fig. 19. Larvae of similar moulting history may be quite different in size within certain limits (see size ranges in section on description of larval stages) and in general morphology. In contrast, the moult is a definitive event and this is represented on the left of the diagram by single lines at the time of each ecdysis. In the centre of the diagram growth is shown with a limited range of values at a given moult. The right of the diagram is evenly divided after stage 3 indicating the continuous process of morphogenesis, 'arrested' at intervals by the hard exoskeleton.

This model for prawn and shrimp development does not apply to all decapods. Knowlton (1974) states that 'Instances of variability are less frequently encountered in Macrura and Anomura, rarely in Brachyura'. The short larval phase of these groups produces a fixed number of moults which are usually morphologically distinct, comparable with the early stages in natant development. Knowlton further speculated that, in general, the degree of larval variation is an index of primitiveness. In the past the phylogeny of the Euphausiacea and Decapoda has been based largely on adult characters but in the light of more larval data it will be possible to re-examine existing classifications and test Knowlton's hypothesis.

Acknowledgments

It is my pleasure to thank the Central Electricity Generating Board for permission to collect on their property, Mr D. Rickard of the Thames Water Authority for his assistance at the West Thurrock site and Miss Ann Gurney for efficiently running the larval rearing unit.

I am most grateful also to the staff at MAFF Fisheries Laboratory, Lowestoft, for allowing me to examine unique collections of inshore plankton samples and in particular I wish to thank Dr D. Harding and Messrs J. Riley and J. Nicholls.

References

Broad, A. C. 1957*a*. Larval development of *Palaemonetes pugio* Holthuis. *Biol. Bull. mar. biol. Lab. Woods Hole* **112** (2) : 144–161.

—— 1957*b*. The relationship between diet and larval development of *Palaemonetes*. *Biol. Bull. mar. biol. Lab. Woods Hole* **112** (2) : 162–170.

Campillo, A., Regnault, M. & Luquet, P. 1975. Évolution de acides nucléiques au cours du développement larvaire de la crevette rose *Palaemon serratus* (Pennant). *Rev. Trav. Inst. Pêch. marit.* **39** (3) : 333–342.

Christiansen, M. E. 1971. Larval development of *Hyas araneus* (Linnaeus) with and without antibiotics (Decapoda, Brachyura, Majidae). *Crustaceana* **21** (3) : 307–315.

Costlow, J. D. 1968. Metamorphosis in crustaceans: 3–41. In: **Etkin, W. & Gilbert, L. I.** (eds), *Metamorphosis: a problem in developmental biology*. North Holland Publishing Co. Amsterdam.

Cviic, V. The bacterial and bacteriostatical action of antibiotics on marine bacteria. 1. Penicillin and streptomycin. *Acta adriat.* **5** (7) : 135–166.

Czerniavsky, W. 1884. Crustacea Decapoda Pontica littoralia. Materialia ad Zoographiam Ponticam comparatam. II. *Trans. Soc. Univ. Kharkow* **13** (suppl.) : 1–268.

Edwards, H. Milne 1837. Histoire naturelle des Crustaces. II. Paris 531 pp.

Faxon, W. A. 1879. On the development of *Palaemonetes vulgaris*. *Bull. Mus. comp. Zool. Harv.* **5** : 303–330.

Fincham, A. A. 1977. Larval development of British prawns and shrimps (Crustacea : Decapoda : Natantia). 1. Laboratory methods and a review of *Palaemon* (*Palaeander*) *elegans* Rathke, 1837. *Bull. Br. Mus. nat. Hist.* (Zool.) **31** (1) : 1–28.

—— 1979. Larval development of British prawns and shrimps (Crustacea : Decapoda : Natantia). 2. *Palaemonetes* (*Palaemonetes*) *varians* (Leach, 1814) and morphological variation. *Bull. Br. Mus. nat. Hist.* (Zool.) **35** (2) : 163–182.

—— **& Williamson, D. I.** 1978. Crustacea, Decapoda: Larvae. VI Caridea, Families Palaemonidae and Processidae. *Fich. Ident. Zooplancton*, 159/160 : 8 pp.

Gurney, R. 1923. Some notes on *Leander longirostris* M. Edwards, and other British prawns. *Proc. zool. Soc. Lond.* 97–123.

—— 1924*a*. The larval development of some British prawns (Palaemonidae) – I. *Palaemonetes varians*. *Proc. zool. Soc. Lond.* 297–328.

—— 1924*b*. The larval development of some British prawns (Palaemonidae). II. *Leander longirostris* and *Leander squilla*. *Proc. zool. Soc. Lond.* 961–982.

— **& Lebour, M. V.** 1941. On the larvae of certain Crustacea Macrura, mainly from Bermuda. *J. Linn. Soc. Lond., Zool.* **41** : 89–181.

Heller, C. 1863. Die Crustaceen des südlichen Europa. Crustacea Podophthalmia. Wilhelm Braumüller, Wien. x, 336 pp.

Holthuis, L. B. 1950. The Palaemonidae collected by the Siboga and Snellius expeditions with remarks on other species. 1. Subfamily Palaemoninae. *Siboga Exped.* **39a** : 1–268.

Hubschman, J. H. 1963. Development and function of neurosecretory sites in the eyestalks of larval *Palaemonetes* (Decapoda : Natantia). *Biol. Bull. mar. biol. Lab. Woods Hole* **125** : 96–113.

Knowlton, R. E. 1974. Larval developmental processes and controlling factors in decapod Crustacea, with emphasis on Caridea. *Thalassia jugosl.* **10** (1/2) : 138–158.

Korschelt, E. 1944. Ontogenie der Decapoden. *Bronns Kl. Ordn. Tierreichs* **5** (1) Bk **7**, Decapoda No. 6 : 671–861.

Little, G. 1969. The larval development of the shrimp, *Palaemon macrodactylus* Rathbun, reared in the laboratory, and the effect of eyestalk extirpation on development. *Crustaceana* **17** : 69–87.

Man, J. G. De 1915. On some European species of the genus *Leander* Desm., also a contribution to the fauna of Dutch waters. *Tijdschr. ned. dierk. Vereen.* Ser. 2, **XIV** : 115–179.

—— 1923. *Leander longirostris* (H. M.-Edw.) var. *robusta* nov. var., the common prawn of the estuary of the Meuse and of the Hollandsch Diep. *Tijdschr. ned. dierk. Vereen.* Ser. 2, **XIX** (1) : 1–9.

Reeve, M. R. 1969. Growth, metamorphosis and energy conversion in the larvae of the prawn, *Palaemon serratus*. *J. mar. biol. Ass. U.K.* **49** : 77–96.

Regnault, M. 1971. Acides aminés libres chez les larves de *Crangon septemspinosa* (Caridea). Variation de leur taux de l'éclosion à la métamorphose. Leur rôle au cours du développement et leur importance dans la nutrition. *Mar. Biol. Berlin* **11** (1) : 35–44.

Sandifer, P. A. 1973. Effects of temperature and salinity on larval development of grass shrimp, *Palaemonetes vulgaris* (Decapoda, Caridea). *Fishery Bull. natn. ocean. atmos. Adm.* **71** : 115–123.

Tsurnamal, M. 1963. Larval development of the prawn *Palaemon elegans* Rathke (Crustacea Decapoda) from the coast of Israel. *Israel J. Zool.* **12** (1–4) : 117–141.

Waddington, C. H. 1953. Epigenetics and evolution. *Symp. Soc. exp. Biol.* **7** : 186–199.

Walne, P. R. 1958. The importance of bacteria in laboratory experiments on rearing the larvae of *Ostrea edulis* (L.). *J. mar. biol. Ass. U.K.* **37** : 415–425.

Wickins, J. F. 1972. Developments in the laboratory culture of the common prawn *Palaemon serratus* (Pennant). *Fishery Invest., Lond.*, Ser. 2, **27** (4) : 23 pp.

Manuscript accepted for publication 20 November 1978

The larval development of the spider crab *Rochinia carpenteri* (Thomson) [Oxyrhyncha : Majidae] with a review of majid subfamilial larval features

R. W. Ingle

Department of Zoology, British Museum (Natural History), Cromwell Road, London SW7 5BD

Synopsis

Two zoeal and a megalopal stage of the N.E. Atlantic deepwater spider crab *Rochinia carpenteri* are described from laboratory-reared material. Subfamilial larval features of the Majidae are reviewed and the larval affinities of *R. carpenteri* are discussed.

Introduction

The deepwater spider crab *Rochinia carpenteri* (Thomson) has been recorded from S. Iceland to N.W. Africa (Christiansen, 1969 : 123) and in depths from about 180 to 1258 m (Hansen, 1908 : 12) on sandy chalk mud (Thomson, 1874 : 176).

In October 1977, five ovigerous crabs were trawled from the Rockall Trough/Hebridean Terrace region of the N.E. Atlantic ocean and transported to the British Museum (Natural History). The larvae hatched by two of these females were successfully reared to the megalopal stage and provide material for the first description of the larval stages of this genus and species.

Materials and methods

The ovigerous crabs were trawled in the Rockall Trough/Hebridean Terrace region of the N.E. Atlantic ocean in the following positions: (*a*) 56°23·1′ N: 09°18·2′ W, 1010–1030 m, Agassiz trawl towed 30 min on 20.10.1977; (*b*) 56°31·7′ N: 09°13·2′ W–56°29·4′ N: 09°11·3′ W, 780–710 m, single warp trawl towed 2 h 28 min on 22.10.1977.

Larvae were reared using methods described by Rice & Ingle (1975 : 104) and Ingle & Clark 1977). Material was fixed in Steedman's solution (Steedman, 1976 : 148) and later transferred to 70% IMS. Drawings and measurements were made with the aid of a *camera lucida*. Measurements given under *Descriptions* are: (*a*) distance between tips of dorsal and rostral spines (T.T.); (*b*) carapace length, from between the eyes to the posterio-lateral carapace margin (C.L.). The material has been registered as BM(NH) 1978: 282–3.

Results

Hatching occurred between 16 and 20 January 1978. An average of 36 days elapsed between hatching and the appearance of megalops. Only a small number of second-stage zoeae successfully moulted to the megalopal stage.

Descriptions

First zoea

Dimensions: T.T. 2·3–3·5 mm; C.L. 1·0–1·2 mm.

Bull. Br. Mus. nat. Hist. (Zool.) **37** (1) : 47–66

Issued 29 November 1979

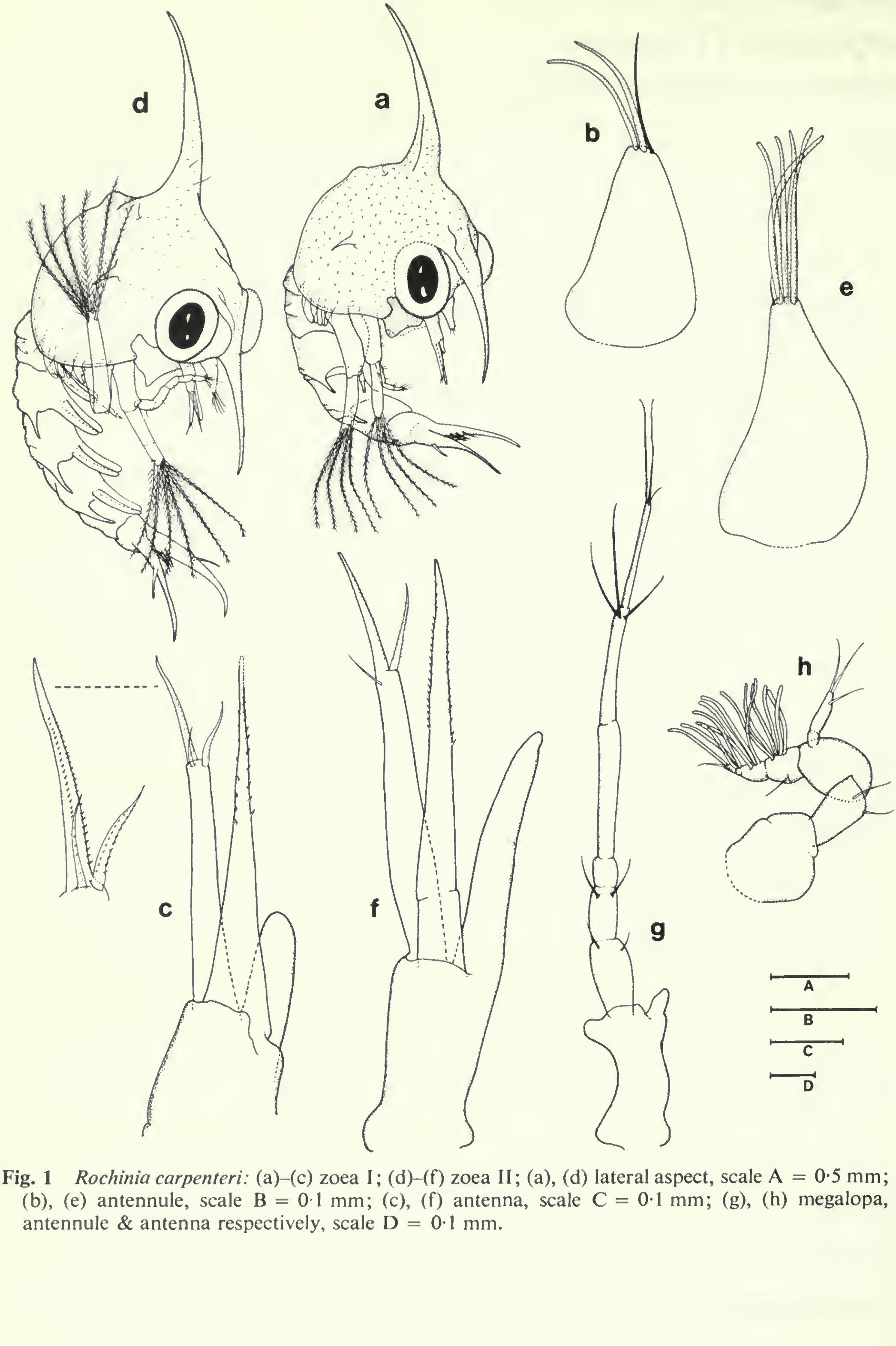


Fig. 1 *Rochinia carpenteri:* (a)–(c) zoea I; (d)–(f) zoea II; (a), (d) lateral aspect, scale A = 0·5 mm; (b), (e) antennule, scale B = 0·1 mm; (c), (f) antenna, scale C = 0·1 mm; (g), (h) megalopa, antennule & antenna respectively, scale D = 0·1 mm.

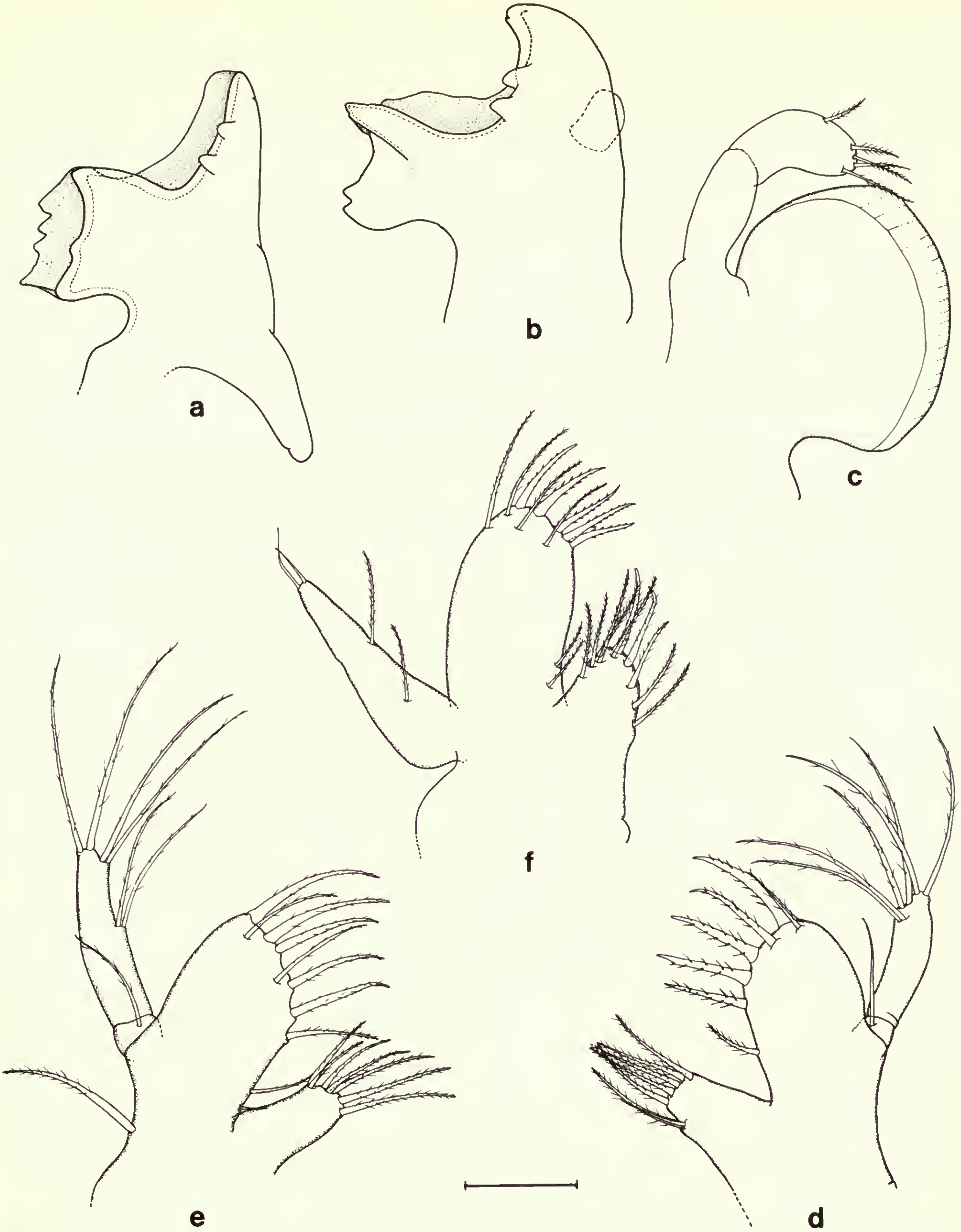


Fig. 2 *Rochinia carpenteri:* ventral aspects of: mandible (a) zoea I, (b) zoea II, (c) megalopa; maxillule (d) zoea I, (e) zoea II, (f) megalopa; scale = 0·1 mm.

CARAPACE (Fig. 1a): Surface punctate, dorsal and rostral spines well developed, slightly curved, narrowing distally; lateral spines well developed. A prominent, broad, median posterio-dorsal tubercule and a pair of posteriorly placed setae; dorso-median elevation of carapace well developed; posterio-lateral margin with a few long spinules arising from inner surface.

EYES: Partly fused to carapace.

ANTENNULE (Fig. 1b): Unsegmented, with 2 terminal aesthestascs and one long seta.

ANTENNA (Fig. 1c): Distal half of spinous process spinulate; exopod reaching well into distal half of spinous process, with 3 terminal spines, longest reaching to apex (or slightly beyond) of spinous process; endopod slightly more than half length of exopod.

MANDIBLE (Fig. 2a): Incisor and molar processes well developed, palp absent.

MAXILLULE (Fig. 2d): Endopod 2-segmented, with 1, 6 setae respectively; distal margin of basal endite with 5 setose spines and 1 seta, inner margin with 1 seta; coxal endite with 7 setae.

MAXILLA (Figs 3a, b): Endopod with large outer and small indistinct inner lobe with 3+3 setae; basal endite with large outer and smaller inner lobe with 4+5 setae; coxal endite bilobed with 4+5 setae; scaphognathite with 12 marginal setae.

FIRST MAXILLIPED (Fig. 4a): Basis with 10 setae (arranged 2, 2, 3, 3); endopod 5-segmented with 3, 2, 1, 2, 4+1 setae; exopod incipiently 2-segmented (in some specimens) with 4 terminal natatory setae.

SECOND MAXILLIPED (Fig. 4c): Basis with 3 setae; endopod 3-segmented, 1st and 2nd segments indistinct, in some specimens, with 0, 1, 4+1 setae; exopod incipiently 2-segmented, with 4 terminal natatory setae.

THIRD MAXILLIPED AND PEREIOPODS: Represented as incipient buds.

ABDOMEN (Figs 5a, b): 5-segmented+telson; second segment with a pair of outwardly directed broad-based, curved, dorso-lateral processes; posterio-lateral processes on segments 3–5 acute, decreasing slightly in size on successive segments, those on fifth angled downwards. A pair of minute setae near posterio-dorsal margin of each segment. Telson forks long, curved and spinulate, each with one long lateral spine; inner posterior margin of telson straight or slightly convex, with 3 pairs of long, plumed setae.

Second zoea

DIMENSIONS: T.T. 3·0–3·2 mm; C.L. 1·3–1·5 mm.

CARAPACE (Fig. 1d): Dorsal spine with few setae near base; posterio-dorsal tubercule larger than in first stage.

EYES: Stalked.

ANTENNULE (Fig. 1e): With 5 aesthetascs and one short seta.

ANTENNA (Fig. 1f): Longest of 3 spines on exopod reaching well beyond distal extremity of spinous process; endopod much more than half length of exopod.

MANDIBLE (Fig. 2b): Molar process longer than in first stage; unsegmented mandibular palp developed.

MAXILLULE (Fig. 2e): Outer margin of basal endite with prominent plumose seta, distal margin with 6 spines and 2 setae, inner margin with 2 setae; coxal endite with 6–7 setae.

MAXILLA (Fig. 3c): Endopod with 4+3 setae; basal endite with 8+5 setae; scaphognathite with 21–23 setae.

FIRST MAXILLIPED (Fig. 4b): Exopod with 6 terminal natatory setae.

SECOND MAXILLIPED (Fig. 4d): Exopod with 6 terminal natatory setae.

THIRD MAXILLIPED AND PEREIOPODS: Represented as incompletely segmented buds.

ABDOMEN (Figs 5c, d): 6-segmented, 6th segment with acute posterio-ventral margin. Additional pairs of minute dorsal setae on segments 3–4 and sometimes on 5; pleopod buds well developed on segments 2–5.

Megalopa

DIMENSIONS: C.L. 2·3–2·5 mm.

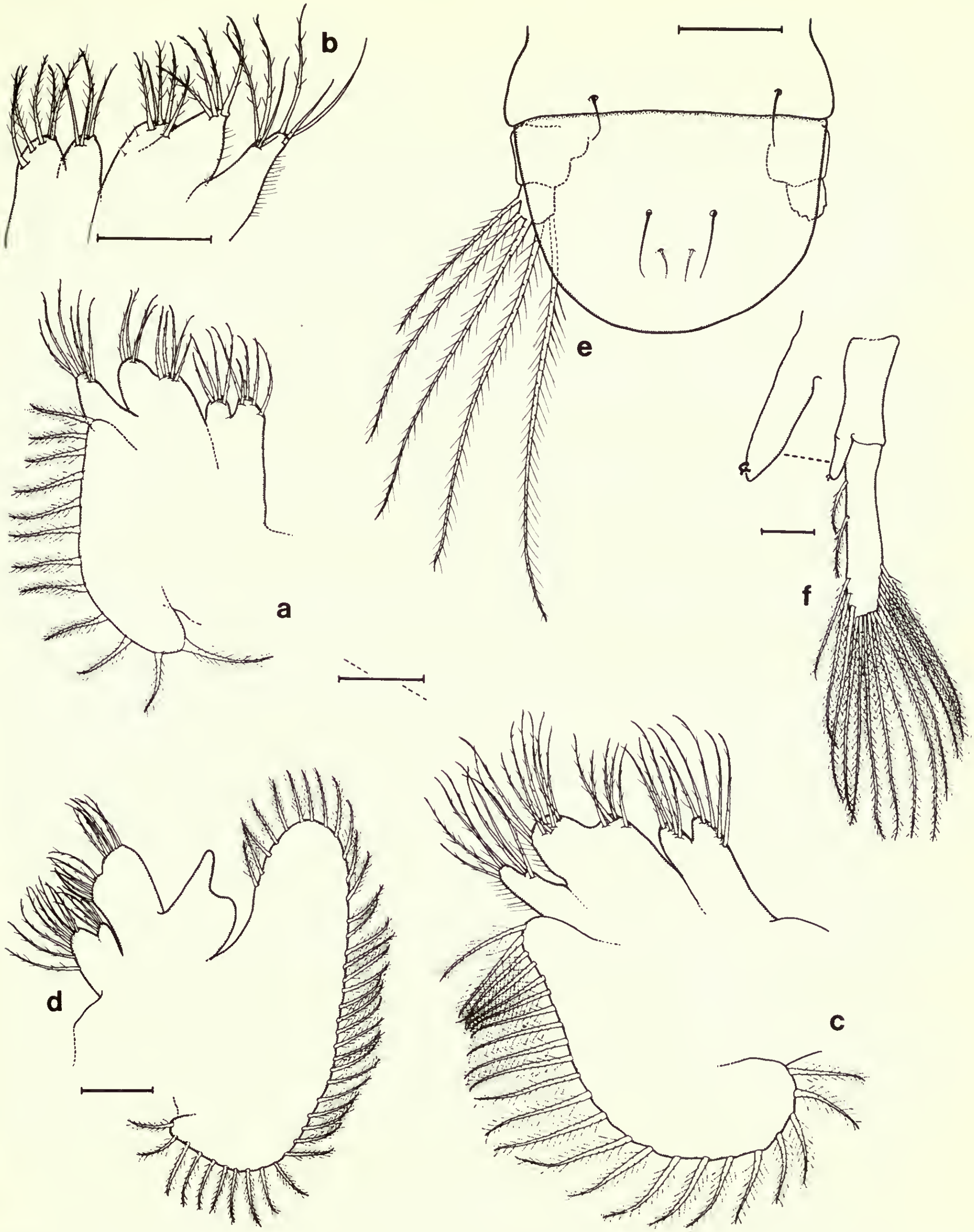


Fig. 3 *Rochinia carpenteri:* maxilla (a) zoea I, (b) terminal portion from another specimen, (c) zoea II, (d) megalopa; (e) telson and left uropod and (f) 1st pleopod of megalopa; scales = 0·1 mm.

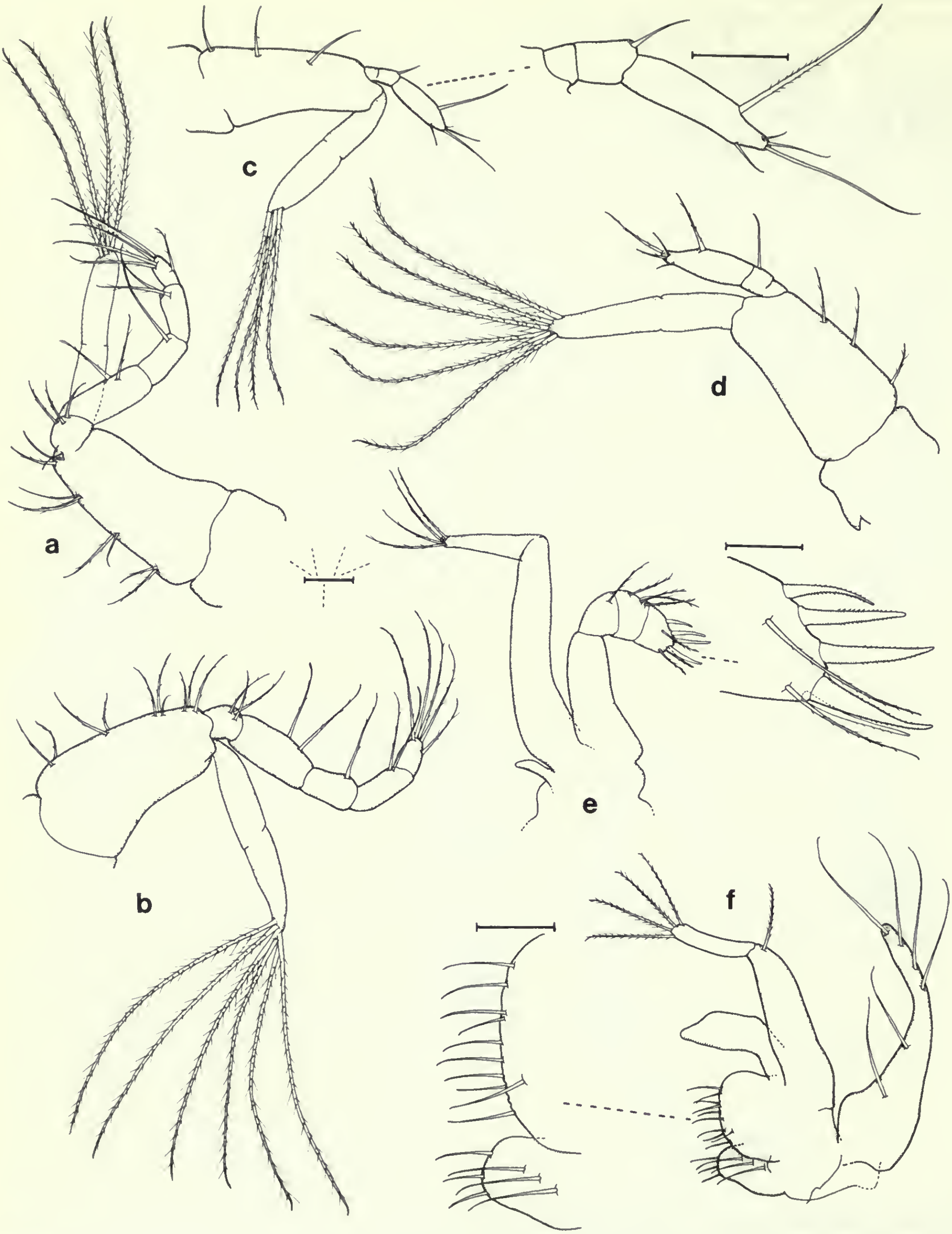


Fig. 4 *Rochinia carpenteri:* 1st maxillipeds (a) zoea I, (b) zoea II, (f) megalopa; 2nd maxillipeds (c) zoea I, (d) zoea II, (e) megalopa; scales = 0·1 mm.

CARAPACE (Figs 7c, d): Longer than broad, anteriorly setose, rostrum long; hepatic regions inflated, each protogastric region with a cristate tubercle; a longitudinal carina on each epibranchial region ending posteriorly in a cristate process; a pair of carinae on metagastric region; each epibranchial/mesobranchial region with an obliquely placed carinae; a very long, stout, median cardiac spine and a small median marginal intestinal tubercle.

EYES: Large, with well-developed cornea.

ANTENNULE (Fig. 1h): Peduncle 3-segmented, 2nd segment with two distally placed setae; exopod with 4–5 incomplete segments, second with 6 aesthetascs, 3rd with 4, 4th with 3, 5th with one aesthetasc and one seta; endopod 2-segmented, distal segment with 3 setae.

ANTENNA (Fig. 1g): Peduncle 3-segmented, first segment with outer lower distal margin produced as acute process, inner upper distal margin with sub-acute expansion; second and third peduncle segments each with 2 distal dorsal median setae; flagellum 4-segmented, third and fourth segments each with 3 setae.

MANDIBLE (Fig. 2c): Incisor process expanded as broad plate with sharp margins, molar process reduced; mandibular palp large, 2-segmented, proximal segment longer than distal, distal with 5 plumose setae.

MAXILLULE (Fig. 2f): Endopod reduced, segmentation indistinct, with 4 setae; distal margin of basal endite with 5–6 setosed spines and 4 setae; coxal endite with 10 setae.

MAXILLA (Fig. 3d): Endopod reduced, basal endite with 6+6 setae, coxal endite with 3–4+9 setae.

FIRST MAXILLIPED (Fig. 4f): Coxa with 6, basis with 10 setae arranged longitudinally. Exopod 2-segmented, proximal with one and distal segment with 4 terminal setae; endopod reduced, unsegmented; epipod well developed, with 6 long setae.

SECOND MAXILLIPED (Fig. 4e): Exopod 2-segmented, distal segment about half length of proximal and with 4 terminal setae; endopod 4-segmented, 2nd segment (carpus) with one and third (propodus) with 4 setae, 4th segment (dactylus) with 4 spines and 3 setae; epipod small.

THIRD MAXILLIPED (Fig. 6a): Coxa/basis with a transverse row of setae. Endopod 5-segmented, inner margin of ischium with irregular serrations, outer surface with 13–15 short setae; outer margin of merus with 2, ventral with 4–5 setae, carpus and propodus with 5 distally placed setae respectively, dactylus with 4 terminal setae. Exopod 2-segmented, distal segment about half length of proximal and with 6–7 terminal setae. Epipod with 5 long setae.

PEREIOPODS (Figs 6b–d, 7a, b): Chelipeds moderately stout, setosed, inner propodal margin with several cristate teeth, inner dactylar margin cristate. Pereipods 2–5 moderately stout, setosed, dactylus terminally thin and curved, inner margin with 3 spines; pereiopods 2–4 with a coxal and ischial spine.

ABDOMEN (Fig. 5e): 6-segmented+telson; with 1–2 pairs of posterio-dorsal setae; posterio-lateral margins of segments rounded, first often with 1–2 setae. Telson broader than long (Fig. 3e), with a pair of dorsal and ventral median setae. Five pairs of pleopods, exopod of first (Fig. 3f) to fourth with 14–16 marginal plumose setae; endopod with 2 coupling hooks; exopod of fifth pleopod (uropod) with 5 long plumose setae.

Review of subfamilial larval features of the Majidae

Larval relationships of genera and species in the Majidae have been discussed by Cano (1893), Lebour (1928, 1931), Aikawa (1937), Bourdillon-Casanova (1960), Yang (1968), Kurata (1969), Italo Campodonico & Leonardo Guzman (1972) and Yang (1976); some studies still await publication (Yang, 1967). There would seem little point in attempting further phylogenetic evaluations until descriptions of the larvae of many more majids become available, particularly of species belonging to the subfamily Majinae, of which only five species have been described, and of the Ophthalmiinae, of which the larval stages of only one species is known. Despite this

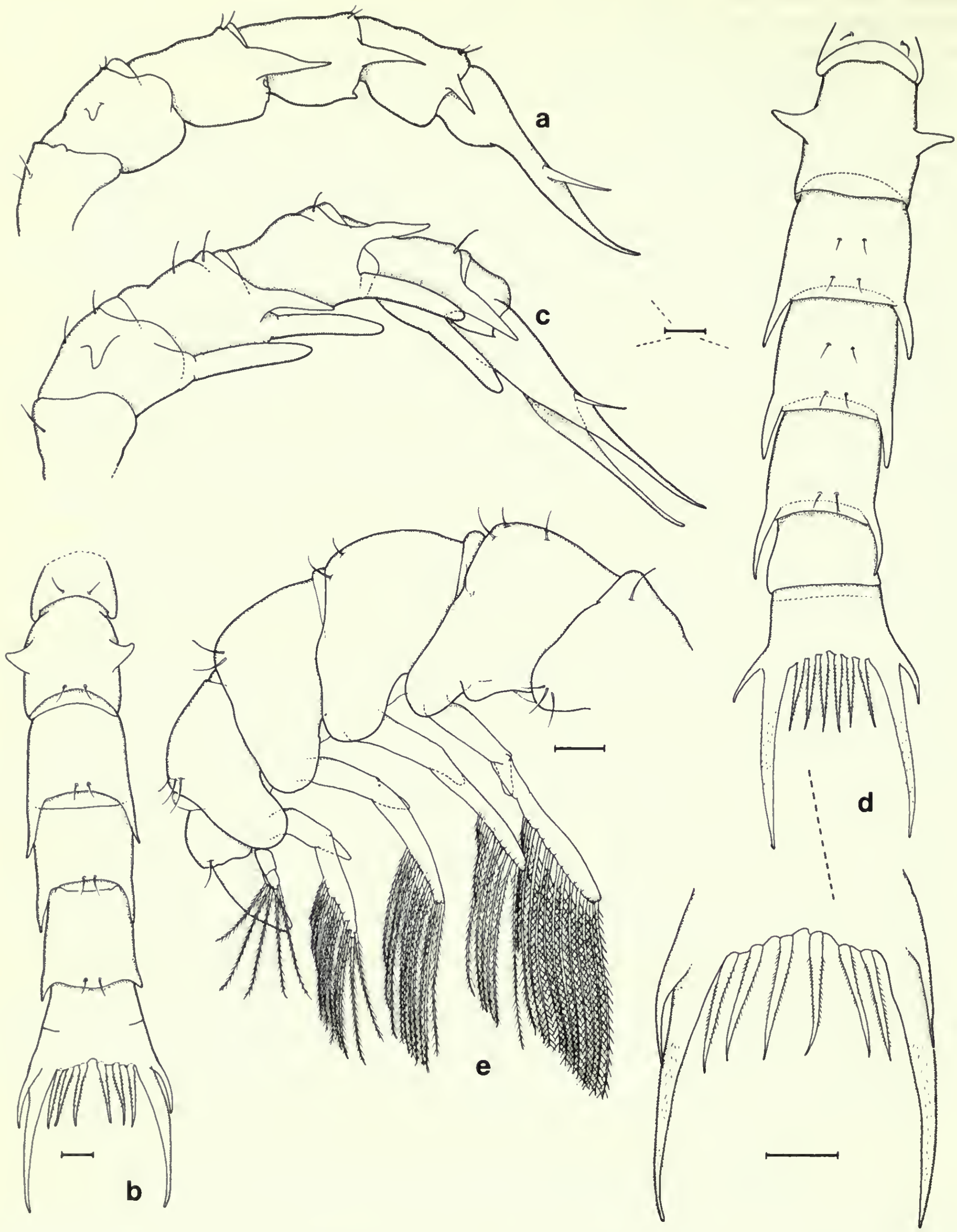


Fig. 5 *Rochinia carpenteri:* abdomens, lateral and dorsal aspects (a), (b) zoea I, (c), (d) zoea II (lower inset of another specimen), (e) megalopa lateral aspect; scales = 0·1 mm.

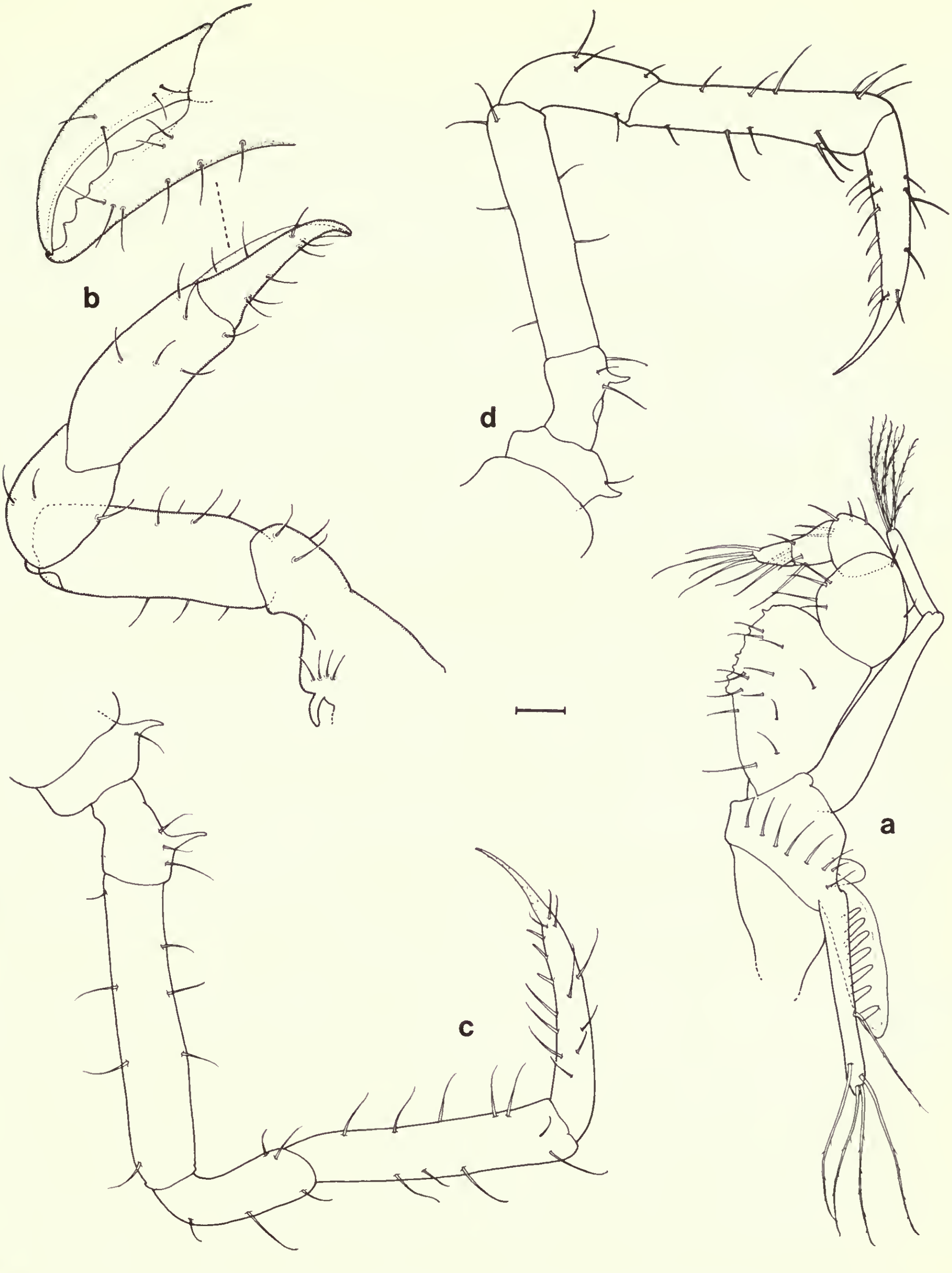


Fig. 6 *Rochinia carpenteri:* megalopa (a) 3rd maxilliped, (b) cheliped, (c) 2nd pereiopod, (d) 3rd pereiopod; scale = 0·1 mm.

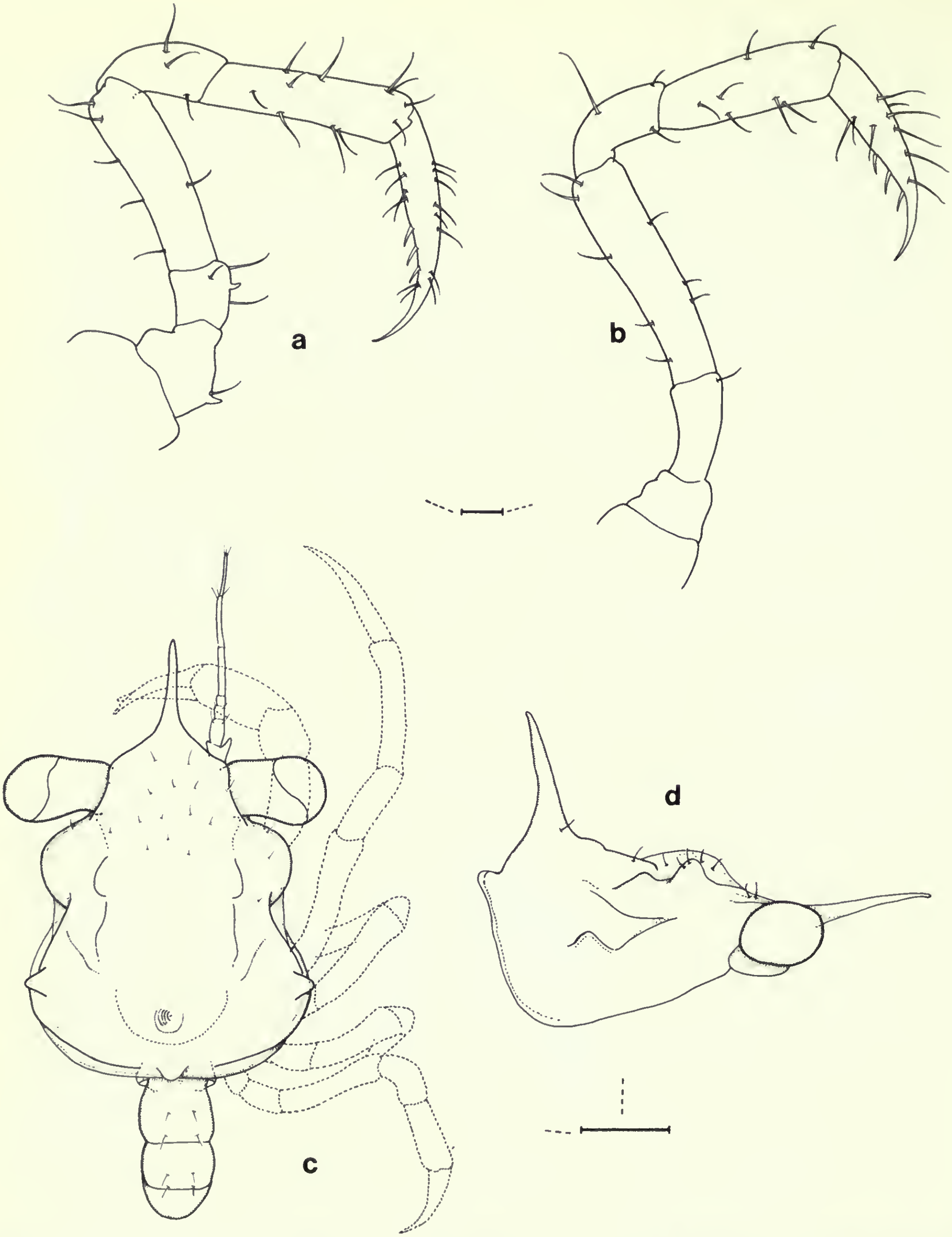


Fig. 7 *Rochinia carpenteri:* megalopa (a) 4th pereiopod, (b) 5th pereiopod, (c) dorsal and (d) lateral aspects of carapace; scales, upper = 0·1 mm, lower = 0·5 mm.

incompleteness it would seem useful to attempt an evaluation of larval characteristics described to date for the Majidae to discover the degree of larval homologies that exist within the currently accepted subfamilial (see Griffin, 1966) classification of the adults. In this appraisal only features are considered that have been sufficiently well illustrated or described for the majority of majid zoeae and megalopae. Some of these (i.e. setation on basal segment of the maxillipeds of zoeae and the presence or absence of pereiopod coxal spines of the megalopae) as well as other features that are not listed here (i.e. setal armature of the maxillule and of the first and second maxilliped endopod of the zoeae) may eventually prove to be of considerable importance, when used in combination with other features, for separating the subfamilies. In general, these above-mentioned features are poorly documented for the majority of previously described majid larvae and only a limited amount of material has been available for verifying some of these features during the course of this present study. A larval bibliography of the Majidae, resulting from this literature appraisal, is given on pp. 59–63.

Subfamily **OREGONIINAE**

Zoea: Carapace lateral spines present; dorsal and rostral spines very long; more than one spine[1] on each telson fork; dorso-lateral processes on 2nd and 3rd abdominal segments; posterio-lateral abdominal processes on 3rd–5th segments often very long; basal segment of 2nd maxilliped with 4–5 setae; antennal exopod with terminal setae.[2]

Megalopa: Rostrum present, not strongly deflected ventrally; submedian spines (carapace spines behind eyes) present; a single or a pair of prominent cardiac spines; basal segment of 2nd pereiopod with a spine; uropods present.

Genera: *Chionoecetes*, *Hyas*, *Oregonia*.

Subfamily **ACANTHONYCHINAE**

Zoea: Carapace lateral spines absent; dorsal and rostral spines very short or absent; only one spine[1] on each telson fork; dorso-lateral processes on 2nd, rarely on 3rd (? *Menaethius*) abdominal segment; posterio-lateral abdominal processes on 3rd–5th segments short or absent; basal segment of 2nd maxilliped with 2–3 marginal setae; antennal exopod with sub-terminal[3] setae.

Megalopa: Rostrum present, strongly deflected ventrally or reduced in size; submedian spines absent; cardiac spine sometimes absent or reduced; basal segment of 2nd pereiopod? without a spine; uropods present.

Genera: *Acanthonyx*, *Epialtus*, *Huenia*, *Menaethius*, *Pugettia*, *Taliepus*.

Subfamily **INACHINAE**

Zoea (group I): Carapace lateral spines absent; dorsal spine of moderate length, sometimes long; rostral spine absent, rarely present (*Naxia*); only one spine[1] on each telson fork; dorso-lateral processes on 2nd, rarely on 3rd (*Stenorhynchus*) abdominal segment; posterio-lateral abdominal processes on 3rd–5th segments sometimes long; basal segment of 2nd maxilliped with not more than 3 marginal setae; antennal exopod with sub-terminal[3] setae.

Megalopa (group I): Rostrum absent (present only in *Stenorhynchus* and strongly deflected ventrally); submedian spines often well developed (except in *Anasimus*); cardiac spines small or absent (except in *Stenorhynchus*); some abdominal segments with dorsal spinules or spinules (except in *Stenorhynchus*); basal segment of 2nd pereiopod ? with or without a spine; uropods absent or vestigial (except in *Stenorhynchus*).

Genera: *Achaeus*, *Anasimus*, *Inachus*, *Macropodia*, *Naxia*, *Stenorhynchus*.

---

[1] Distinction is not made here between lateral and dorsal spines or spinules as this difference is not always clearly shown in some illustrations.

[2] This implies that the exopod terminates in 2 or 3 spines or setae of equal thickness but not necessarily of equal length.

[3] This implies that the exopod terminates in a short movable or non-movable stout spine from the base of which arise one or two setae, usually shorter than the length of the spine.

ZOEA (group II): Carapace lateral spines present; dorsal spine of moderate length; rostral spine of moderate length often short; more than one spine[1] on each telson fork; dorso-lateral processes on 2nd and 3rd abdominal segments; posterio-lateral abdominal processes on 3rd–5th segments sometimes short; basal segment of 2nd maxilliped with not more than 3 marginal setae; antennal exopod with terminal[2] setae.

MEGALOPA (group II): Rostrum present, strongly deflected ventrally or straight; submedian spines developed or reduced; cardiac spine short or long; abdominal segments without dorsal spines; basal segment of 2nd pereiopod with or ? without spines; uropods present.

GENERA: *Eurypodius*, *Macrocheira*, *Pleistacantha*, *Camposcia*.

Subfamily **PISINAE**

ZOEA: Carapace lateral spines absent; dorsal spine of moderate length; rostral spine of moderate length often short; only one spine[1] on each telson fork; dorso-lateral processes on 2nd abdominal segment, rarely on 3rd (*Herbstia*); posterio-lateral processes on 3rd–5th abdominal segments often short; basal segment of 2nd maxilliped with not more than 3 marginal setae; antennal exopod with sub-terminal[3] setae.

MEGALOPA: Rostrum present often straight; submedian spines absent; cardiac spine absent (except in *Libinia*); basal segment of 2nd pereiopod without a spine; uropods present.

GENERA: *Eurynome*, *Herbstia*, *Hyastenus*, *Libidoclaea*, *Libinia*, *Lissa*, *Naxioides*, *Pisa*, *Pisoides*.

Sub family **MAJINAE**

ZOEA (group I): Carapace lateral spines present; dorsal spine often well developed and usually of moderate length; rostral spine prominent, of moderate length; more than one spine[1] on each telson fork; dorso-lateral processes on 2nd and 3rd abdominal segments (? absent on 3rd in *Maja verrucosa*); posterio-lateral processes on 3rd–5th abdominal segments prominent sometimes long; basal segment of 2nd maxilliped with not more than 3 marginal setae; antennal exopod with terminal[2] setae.

MEGALOPA (group I): Rostrum present and moderately well developed, slightly deflected ventrally; submedian spines or processes present; cardiac spine not prominent; basal segment of 2nd pereiopod with spines; uropods present.

GENERA: *Maja*, *Schizophrys*.

ZOEA (group II): Carapace lateral spines absent; dorsal spine sometimes reduced or absent; rostral spine sometimes reduced; more than one spine[1] on each telson fork; dorso-lateral processes only on 2nd abdominal segment; posterio-lateral processes on 3rd–5th abdominal segments sometimes short; basal segment of 2nd maxilliped ? with not more than 3 marginal setae; antennal exopod with terminal[2] setae.

MEGALOPA (group II): Rostrum present, sometimes small; submedian spines or processes sometimes absent; cardiac spine small; basal segment of 2nd pereiopod with a spine; uropods present.

GENERA: *Leoptomithrax*, *Acanthophrys*.

Subfamily **OPHTHALMIINAE**

ZOEA: Carapace lateral spines present; dorsal spine very short; rostral spine very short; more than one spine[1] on each telson fork; abdominal dorso-lateral processes absent; ? 3 prominent dorso-lateral setae on 1st abdominal segment; posterio-lateral processes on 3rd–5th abdominal segments absent; basal segment of 2nd maxilliped ? without setae; antennal exopod with terminal[2] setae.

MEGALOPA: Rostrum present, well developed, straight; submedian spines or processes absent; cardiac spine absent; basal segment of 2nd pereiopod ? without spines.

GENERA: *Stilbognathus*

Subfamily **MITHRACINAE**

ZOEA (group I): Carapace lateral spines absent; dorsal spine of moderate length; rostral spine short; only one spine[1] on each telson fork; dorso-lateral process on 2nd abdominal segment; posterio-lateral processes on 3rd–5th abdominal segments sometimes short; basal segment of 2nd maxilliped ? without setae; antennal exopod with sub-terminal[3] setae (? except in *Mithrax*).

MEGALOPA (group I): Rostrum present, deflected slightly ventrally; submedian processes present; cardiac spine reduced; basal segment of 2nd pereiopod ? without spines; uropod present.

GENERA: *Microphrys*, *Mithrax*, *Tiarinia*.

ZOEA (group II): Carapace lateral spines present; dorsal spine absent; rostral spine of moderate length; more than one spine[1] on each telson fork; dorso-lateral processes on 2nd–3rd abdominal segments; posterio-lateral abdominal processes on 3rd–5th segments short; basal segment of 2nd maxilliped ? without setae; antennal exopod with sub-terminal[3] setae.

MEGALOPA (group II): Rostrum present, deflected slightly ventrally; submedian processes absent; cardiac spine absent or reduced; basal segment of 2nd pereiopod with a spine; uropods present.

GENUS: *Micippa*.

The subfamilial larval features listed above reveal considerable degrees of apparent phylogenetic homology within three of the six subfamilies (i.e. Oregoniinae, Acanthonychinae and Pisinae) of the Majidae. This homology is less clear within the remaining subfamilies except, perhaps, the Inachinae in which two groups can be recognized that correspond to the divisions of this subfamily proposed by Balss (1929), the Camposcioidea (group I) and the Macrocheiroidea (group II). These divisions were partly (see Garth, 1958) and totally (see Griffin, 1966) rejected by subsequent workers because of the difficulties in interpreting homologies of orbital spines in genera and species assigned to one or the other group. Similar relationships of larvae attributed to the subfamilies Majinae and Mithracinae are not apparent at present and no doubt reflect our limited larval knowledge of these two subfamilies. Nevertheless, this present evaluation seems to suggest multiple phylogenetic lineage for both subfamilies and perhaps similar to that shown for the Inachinae.

Larval affinities of *Rochinia carpenteri*

In having prominent lateral spines on the carapace and ten setae on the basis of the first maxilliped, the first zoea of *R. carpenteri* shows affinities to the Oregoniinae rather than to the other subfamilies of Majidae in which the lateral spines are sometimes absent and in which the first maxilliped basis often has less than ten setae. The single spine on each fork of the telson and the sub-terminal setae on the antennal exopod place the zoea of *R. carpenteri* near to the Acanthonychinae, some group I Inachinae and to the Pisinae. Its affinities to the Pisinae are further strengthened by the setal armature of the first maxilliped basis (10) and the moderately developed spinous processes of the posterio-lateral margins of the third to fifth abdominal segments. The megalopa of *R. carpenteri* is more difficult to assign but the well developed rostral spine, the absence of submedian spines or processes and the prominent cardiac spine all suggest tenuous affinities to some inachinid (i.e. *Macrocheira*) and pisinid (i.e. *Libinia*) megalops.

Larval bibliography of the family Majidae

OREGONIINAE

Chionoecetes bairdi Rathbun
Haynes, 1973 : 769, figs 1–2 (prezoea, 1st zoea); Jewett & Haight, 1977 : 459 (megal.)

Chionoecetes japonicus Rathbun
Motoh, 1970 : 7 (descript prezoea & 1st zoea); Motoh, 1976 : 533, figs 1–4 (1st, 2nd zoeae, megal.)

Chionoecetes opilio (Fabricius)
non Stephensen, 1935 : 40, fig. 16 (= ? *Geryon sp.*); Aikawa, 1935 : 222, Pl. I, fig. 5 (prezoea); Aikawa, 1937 : III, fig. 17 (prezoea); Kurata, 1963 : 25, fig. 1 (1st, 2nd zoeae, megal.); Kon, 1967 : 727, fig. 1, Pl. I (prezoea, 1st zoea); Ito, 1968 : 91 (descript. prezoea); Kuwatani *et al*, 1971 : 32, Pls 1–3 (prezoea, 1st zoea as *C. opilio elongatus*); Kuwatani *et al.*, 1973 : 93, fig. 1 (prezoea); Haynes, 1973 : 774, fig. 2l, m (1st zoea); Motoh, 1973 : 1223, figs 1–4 (1st, 2nd zoea, megal.)

Hyas araneus (Linnaeus)
Bjorck, 1913 : 22, figs 1, 2 (megal. as *H. coarctatus*); Williamson, 1915 : 526, figs 424–5 (megal. after Björck as *Inachus coarctatus*); Lebour, 1928 : 544, Pl. XIV, fig. 10 (1st crab as *H. coarctatus*); Lebour, 1931 : 93, Pl. II, fig. 1 (1st zoea); Christiansen, 1973 : 67, figs 1A–19A (1st, 2nd zoeae, megal. 1st, 2nd crab)

Hyas coarctatus Leach
Williamson, 1911 : 13, Pl. I, figs 1, 2, Pl. V, figs 70–81, 83 (1st, 2nd zoea, megal. 1st crab as *H. araneus*); Stephensen, 1912 : 127, fig. 33 (1st zoea as Brachyurid-larvae); Williamson, 1915 : 521, figs 409–417 (1st, 2nd zoeae as *Inachus araneus*); Williamson, 1915 : 526, figs 420–423, 426–429 (1st, 2nd zoeae); Stephensen, 1917 : 241, fig. 1 (2nd zoea); Lebour, 1928 : 544, fig. 4 (14–15), fig. 5 (29–30) Pl. II, fig. 9, Pl. XIV, figs 8–9 (1st, 2nd zoeae, megal); Kurata, 1963 : 28, fig. 2 (1st, 2nd zoea, megal. as *H. coarctatus alutaceus*); Christiansen, 1973 : 67, figs 1B–19B (1st, 2nd zoea, megal. 1st, 2nd crab)

Hyas lyratus Dana
Hart, 1960 : 542, figs 29–38 (1st, 2nd zoeae, megal.)

Oregonia gracilis Dana
Hart, 1960 : 540, figs 1–28 (1st, 2nd zoeae, megal.)

ACANTHONYCHINAE

Acanthonyx lunulatus (Risso)

Cano, 1893 : 539, Tav. 35, figs 60–63 (2nd zoea as *Acanthonyx* sp.); Boraschi, 1921 : 8, Tav. I, fig. 4 (1st zoea); Bourdillon-Casanova, 1960 : 214, fig. 73 (1st, 2nd zoeae); Heegaard, 1963 : 482, figs 112–118, Pl. XVII, fig. 21 (1st zoea)

Acanthonyx petiverii H. Milne Edwards
Lebour, 1944 : 120, fig. 10 (1st zoea)

Epialtus dilatatus A. Milne Edwards
Yang, 1968 : 181, figs 1–8 (1st, 2nd zoeae, megal. 1st crab)

Huenia proteus de Haan
Aikawa, 1935 : 220, Pl. I, fig. 4 (1st zoea); Aikawa, 1937 : 108, fig. 15 (1st zoea); Kurata, 1969 : 98, fig. 11 (1st zoea)

Menaethius monoceros (Latreille)
Gohar & Al-Kholy, 1957 : 194, Pl. VIII (1st, 2nd zoeae, megal.)

Pugettia gracilis (Dana)
Forss & Coffin, 1960 : 4, Pls III, IV (1st zoea, megal.)

Pugettia incisa (de Haan)
Kurata, 1969 : 96, figs 9, 10 (1st zoea, megal.)

Pugettia quadridens (de Haan)
Aikawa, 1927 : 270, Pl. I (1st zoea); Aikawa, 1929 : 38, Pl. III, fig. 19, Pl. IV, figs 25, 33 (1st zoea); Kurata, 1969 : 94, figs 7, 8 (1st zoea, megal.); Iwata, 1970 : 189, fig. 1, Pl. I–II (prezoea, 1st zoea)

Taliepus dentatus (A. Milne Edwards)
Fagetti & Campodonico, 1971 : 1, figs 1–3 (1st, 2nd zoea, megal.)

INACHINAE

Achaeus cranchii Leach
Bocquet, 1954 : 50, figs 1–4 (1st, 2nd zoeae, megal.)

Achaeus tuberculatus Miers
Kurata, 1969 : 87, figs 2, 3 (1st zoea, megal. 1st crab)

Achaeus spp.
Aikawa, 1935 : 218, 219, Pl. I, figs 1, 2 (1st zoeae); Aikawa, 1937 : 107, 108, figs 13, 14 (1st zoeae); Bourdillon-Casanova, 1960 : 220, figs 76–77 (megal. 1st crab)

Anasimus latus Rathbun
Sandifer & van Engel, 1972 : 141, figs 1–4 (1st, 2nd zoeae, megal.)

Camposcia retusa Latreille
Gohar & Al-Kholy, 1957 : 189, figs 1–3 (1st, 2nd zoeae, megal.)

Eurypodius latreillei Guérin
Italo Campodonico & Leonardo Guzman, 1972 : 233, figs 1–4 (1st, 2nd zoeae, megal.)

Inachus dorsettensis (Pennant)
Claus, 1876: Taf. X, fig. 8 (1st zoea as *I. scorpio*); non Cano, 1893: Tav. 35, fig. 71 (1st zoea as *I. scorpio* = *I. thoracicus*); non Williamson, 1915 : 530, fig. 430 (1st zoea after Cano = *I. thoracicus*); Lebour, 1927 : 802, Pls I–IV (prezoea, 1st, 2nd zoeae, megal. 1st crab); Lebour, 1928 : 546, Pl. III, fig. 5, Pl. XV, figs 4–5 (prezoea, 1st, 2nd zoeae, megal. 1st–3rd crab); Heegaard, 1963 : 471, figs 70–76, Pl. XVII, fig. 15 (1st zoea); Ingle, 1977 : 331, figs 1–10 (1st, 2nd zoeae, megal. 1st–3rd crab)

Inachus leptochirus Leach
Lebour, 1928 : 548, Pl. III, fig. 7, Pl. XIV, figs 11, 13, Pl. XV, figs 1, 2 (1st, 2nd zoeae, megal. 1st crab)

Inachus phalangium (Fabricius)
Gourret, 1884 : 17, Pl. I, figs 5–6 (1st zoea as *I. dorynchus*); Williamson, 1915 : 531, figs 431–432 (1st zoea as *I. dorynchus* after Gourret); Lebour, 1928 : 547, Pl. III, fig. 6, Pl. XIV, fig. 12, Pl. XV, fig. 3 (1st, 2nd zoeae, megal. as *I. dorynchus*)

Inachus thoracicus Roux
Heegaard, 1963 : 474, figs 77–83, Pl. XVII, fig. 16 (1st zoea)

Inachus spp.
Bourdillon-Casanova, 1960 : 215, figs 74–75 (megals, 1st crab)

Macrocheira kaempferi de Haan
Aikawa, 1941 : 119, fig. 2 (1st zoea); Tanase, 1967 : 303, figs 1–3 (1st, 2nd zoeae, megal.); Kurata, 1969 : 89, figs 4–5 (1st zoea, megal.)

Macropodia deflexa Forest
Lebour, 1928 : 550, Pl. III, fig. 9, Pl. XV, fig. 6, Pl. XVI, figs 1, 2, 7 (prezoea, 1st, 2nd zoeae, megal. 1st crab as *M. egyptia*)

Macropodia rostrata (Linnaeus)
Thompson, 1836 : 371, fig. 1e (1st zoea as *M. phalangium*); Cano, 1893: Tav. 35, figs 70–74, 77–83 (1st zoea, megal. crab stage as *Stenorhynchus phalangium*); Lo Bianco, 1904 : 33, Taf. XII, fig. 43 (1st crab as *S. phalangium*); Lebour, 1928 : 550, Pl. III, fig. 10, Pl. XV, fig. 7, Pl. XVI, figs 3, 5, 8 (prezoea, 1st, 2nd zoeae, megal. 1st crab)

Macropodia tenuirostris (Leach)
Lebour, 1927 : 806, Pl. I, figs 2, 8, Pl. II, fig. 2, Pl. III, figs 2, 4, 5 (prezoea, 1st, 2nd zoeae, megal. 1st crab as *M. longirostris*)

Naxia hystrix Miers
Aikawa, 1935 : 222, Pl. I, fig. 6 (1st zoea); Aikawa, 1937 : 109, fig. 16 (1st zoea)

Paratymolus pubescens Miers
Aikawa, 1937 : 106, fig. 12 (1st zoea)

Pleistacantha sancti-johanis Miers
Aikawa, 1935 : 220, Pl. I, fig. 3 (1st zoea); Aikawa, 1937 : 105, fig. 11 (1st zoea); Kurata, 1969 : 92, fig. 6 (1st zoea)

Stenorhynchus seticornis (Herbst)
Yang, 1976 : 158, figs 1–9 (1st, 2nd zoeae, megal. 1st crab)

Stenorhynchus sp.
Yang, 1976 : 168, figs 11–13 (1st zoea)

PISINAE

Doclea gracilipes Stimpson
Chhapgar, 1959 : 48, fig. 11 (megal.)

Eurynome aspera (Pennant)
*Kinahan, 1858 : 233 (prezoea); *Kinahan, 1860 : 73, Pl. 9, figs 4–6 (? 1st zoea); Cano, 1893 : Taf. 35, figs 57–59 (1st zoea as *Eurynome sp.*); *Gurney, 1924 : 433, figs 1–2 (prezoea, 1st zoea); *Lebour, 1928 : 543, fig. 5 (31), Pl. II, fig. 8, Pl. XIV, figs 2–5 (1st, 2nd zoeae, megal. 1st crab); Bourdillon-Casanova, 1960 : 204, fig. 67a (megal.)

Herbstia condyliata (Herbst)
Cano, 1893 : Tav. 35, figs 52–56 (2nd zoea, megal.); Bourdillon-Casanova, 1960 : 205, fig. 68 (1st zoea)

Hyastenus diacanthus (de Haan) Kurata, 1969 : 101, figs 13–14 (1st zoea, megal.)

Libidoclaea grandaria H. Milne Edwards & Lucas
Fagetti, 1969 : 131, figs 1–4 (1st, 2nd zoeae, megal.)

Libinia dubia H. Milne Edwards
Sandifer & van Engel, 1971 : 18, figs 1–4 (1st, 2nd zoeae, megal.)

Libinia emarginata Leach
Johns & Lang, 1977 : 831, figs 1–5 (1st, 2nd zoeae, megal.)

Libinia setosa Lockington
Rathbun, 1923 : Pl. XXXVI, fig. 1 (megal.)

Libinia spinosa H. Milne Edwards
Boschi & Scelzo, 1968 : 170, figs 1–42 (1st, 2nd zoeae, megal.)

Lissa chiragra (Herbst)
Cano, 1893 : Tav. 35, figs 45–51 (1st, 2nd zoeae, megal. 1st crab as *Lissa sp.*); Boraschi, 1921 : 8, Tav. 1, fig. 15 (1st zoea); Bourdillon-Casanova, 1960 : 212, fig. 72 (1st zoea); Heegaard, 1963 : 480, figs 105–111, Pl. XVII. fig. 20 (1st zoea)

Naxioides histrix (Miers)
Kurata, 1969 : 100, fig. 12 (1st zoea)

Naxioides serpulifera (Guérin)
Rathbun, 1914 : 661, Pl. II, figs 9–10 (1st, 2nd crab, direct develop.)

Pisa armata (Latreille)
Lebour, 1931 : 94, Pl. II, fig. 2, Pl. I, figs 2–5 (1st, 2nd zoeae as *P. biaculeata*); Bourdillon-Casanova, 1960 : 207, fig. 69 (megal. as *P. gibbsi*); Heegaard, 1963 : 476, figs 84–90, Pl. XVII, fig. 17 (1st zoea)

Pisa corallina (Risso)
Gourret, 1884 : 15, Pl. II, figs 3–5 (1st zoea)

---

* Identity uncertain because of confusion with *E. spinosa* (see Hartnoll, 1961).

Pisa nodipes Leach
Heegaard, 1963 : 479, figs 98–104, Pl. XVII, fig. 19 (1st zoea)

Pisa tetraodon (Pennant)
Heegaard, 1963 : 477, figs 84–90, Pl. XVII, fig. 18

Pisa spp.
Cano, 1893 : Tav. 35, figs 41–44 (1st, 2nd zoeae, megal.? crab stage); Bourdillon-Casanova, 1960 : 210, fig. 70 (1st zoeae, megal.)

Pisoides edwardsi (Bell)
Fagetti, 1969*a* : 160, figs 1–3 (1st, 2nd zoeae, megal.)

Pisoides ortmanni (Balss)
Kurata, 1969 : 103, figs 15, 16 (1st zoea, megal.)

MAJINAE

Acanthophrys longispinosus (de Haan)
Kurata, 1969 : 111, figs 22, 23 (1st zoea, megal.)

Leptomithrax bifidus Ortmann
Kurata, 1969 : 106, figs 18, 19 (1st zoea, megal.)

Leptomithrax edwardsi (de Haan)
Kurata, 1969 : 105, fig. 17 (1st zoea)

Maja squinado (Herbst)
Schlegel, 1911 : 480 (1st, 2nd zoeae, megal. descript. only); Lebour, 1927 : 809, Pl. I, figs 3, 9, Pl. II, figs 3, 9, Pl. II, figs 3, 9, Pl. IV, figs 9–15 (prezoea, 1st, 2nd zoeae, megal. not crab stages = portunids); Lebour, 1928 : 542, figs 2 (1–2), Pl. II, fig. 7, Pl. XIV, figs 6–7 (1st, 2nd zoeae, megal. not 1st–3rd crab = portunids); Bourdillon-Casanova, 1960 : 203, fig. 66 (megal.)

Maja verrucosa H. Milne Edwards
Cano, 1893: Tav. 34, figs 26–28 (not fig. 29 = *Sirpus*, see Gordon 1953), fig. 30, Tav. 35, fig. 86 (1st, 2nd zoeae, megal. crab stage); Bourdillon-Casanova, 1960 : 202 (cf 1st, 2nd zoeae with *M. squinado*); Heegaard, 1963 : 484, figs 119–126, Pl. XVII, fig. 22 (1st zoea)

Schizophrys aspera (H. Milne Edwards)
Kurata, 1969 : 108, figs 20, 21 (1st zoea, megal.)
Majinae
Rice & Williamson, 1977 : 41, fig. 17 (2nd zoea)

OPHTHALMIINAE

Stilbognathus erythraceus von Martens
Al-Kholy, 1959 : 240, figs 1–21 (2nd zoea, megal.)

MITHRACINAE

Micippa thalia (Herbst)
Kurata, 1969 : 113, figs 24, 25 (1st zoea, megal.)

Microphrys bicornutus (Latreille)
Lebour, 1944 : 122, fig. 12 (1st, 2nd zoeae); Hartnoll, 1964 : 241, figs 1–3 (prezoea, 1st, 2nd zoeae)

Mithrax forceps A. Milne Edwards
Lebour, 1944 : 121, fig. 11 (1st zoea)

Mithrax spinosissimus (Lamarck)
Provenzano & Brownell, 1977 : 735, figs 1–7 (1st, 2nd zoeae, megal. 1st crab)

Tiarinia cornigera Latreille
Aikawa, 1937 : 112, fig. 18 (1st zoea); Kurata, 1969 : 115, fig. 26 (1st zoea)

Acknowledgments

I wish to thank Dr John Gordon for allowing me to participate in Leg 1 of Cruise 16/17 of RRS *Challenger*, for providing facilities on board and for his generous help throughout the cruise. I also wish to express my sincere gratitude to Capt. Maw and his officers for their willing and able assistance in obtaining this material in spite of the difficult circumstances that frequently prevailed during this particular cruise. Finally, I wish to thank Dr A. L. Rice for his valued discussions throughout the preparation of this manuscript.

References

Aikawa, H. 1927. On the morphology of crab zoeal stages. *Proc. scient. Fishery Ass., Tokyo* **4** : 270–296 (not seen).

—— 1929. On larval forms of some Brachyura. *Rec. oceanogr. Wks Japan* **2** : 17–55.

—— 1935. [Inachidae zoea: Larval characters of the family Inachidae and allied forms.] *Zool. Mag. Tokyo* **42** : 217–227. (In Japanese.)

—— 1937. Further notes on brachyuran larvae. *Rec. oceanogr. Wks Japan* **9** : 87–162.

—— 1941. Additional notes to brachyuran larvae. *Rec. oceanogr. Wks Japan* **12** : 117–120.

Al-Kholy, A. A. 1959. Larval stages of four brachyuran crustacea (from the Red Sea). *Publs mar. biol. Stn Ghardaga* **10** : 239–246.

Balss, H. 1929. Decapoden des Roten Meeres. IV. Oxyrhyncha und Schlussbetrachtungen in: *Expedition S.M. Schiff "Pola" in das Rote Meer. Zool. Ergenb.* **36** : 1–30, Wien.

Björck, W. 1913. Biologisch-faunistische Untersuchungen aus dem Oresund. I. Pantopoda, Mysidacea und Decapoda. *Acta Univ. lund.* **9** 2 : 1–39.

Bocquet, C. 1954. Développement larvaire d'*Achaeus cranchii* Leach (Decapode Oxyrhynque). *Bull. Soc. zool. Fr.* **79** : 50–56.

Boraschi, L. 1921. Osservazioni sulle larve dei Crostacei Decapodi. *Memorie R. Com. talassogr. ital.* **87** : 1–32.

Boschi, E. E. & Scelzo, M. A. 1968. Larval development of the spider crab *Libinia spinosa* H. Milne Edwards, reared in the laboratory (Brachyura, Majidae). *Crustaceana* (Suppl. 2) : 170–180.

Bourdillon-Casanova, L. 1960. Le meroplancton du Golfe de Marseille: Les larves de crustacés decapodes. *Recl. Trav. Stn. mar. Endoume* **30** 18 : 1–286.

Cano, G. 1893. Sviluppo e Morfologie degli Oxyrhynchi. *Mitt. zool. Stn. Neapel* **10** : 527–583.

Chhapgar, B. F. 1959. On the breeding habits and larval stages of some crabs of Bombay. *Rec. Indian Mus.* **54** : 33–52.

Christiansen, M. E. 1969. *Marine invertebrates of Scandinavia, No. 2. Crustacea, Decapoda, Brachyura.* Universitetsforlaget, Oslo 1–143, Oslo.

—— 1973. The complete larval development of *Hyas araneus* (Linnaeus) and *Hyas coarctatus* Leach (Decapoda, Brachyura, Majidae) reared in the laboratory. *Norw. J. Zool.* **21** : 63–89.

Claus, C. 1876. *Untersuchungen zur Erforschung der Genealogischen Grundlage des Crustaceen-Systems.* i-ciii + 114 pp., Wien.

Fagetti, E. 1969. The larval development of the spider crab *Libidoclaea granaria* H. Milne Edwards & Lucas under laboratory conditions (Decapoda, Brachyura : Majidae, Pisinae). *Crustaceana* **12** : 131–140.

—— 1969*a*. Larval development of the spider crab *Pisoides edwardsi* (Decapoda, Brachyura) under laboratory conditions. *Mar. Biol. Berlin* **4** : 160–165.

—— **& Campodonico, I.** 1971. Desarrollo larval en el laboratorio de *Taliepus dentatus* (Milne-Edwards) (Crustacea Brachyura : Majidae, Acanthonychinae). *Revta Biol. mar.* **14** : 1–14.

Forss, C. A. & Coffin, H. G. 1960. The use of the brine shrimp nauplii, *Artemia salina*, as food for the laboratory culture of decapods. *Walla Walla Coll. Publs Dep. biol. Sci.* **26** : 1–15.

Garth, J. S. 1958. Brachyura of the Pacific coast of America Oxyrhyncha. *Allan Hancock Pacif. Exped.* **21** : 1–854.

Gohar, H. A. F. & Al-Kholy, A. A. 1957. The larvae of some brachyuran crustacea (from the Red Sea). *Publs mar. biol. Stn Ghardaga* **9** : 145–202.

Gordon, I. 1953. On *Sirpus*, a genus of pigmy Cancroid Crabs. *Bull. Br. Mus. nat. Hist.* (Zool.) **2** : 43–65

Gourret, P. 1884. Considérations sur la faune pélagique du Golfe de Marseille. Première partie. *Annl. Mus. Hist. nat. Marseilles* **11** (2) : 12–101.

Griffin, D. J. G. 1966. A review of the Australian majid spider crabs (Crustacea, Brachyura). *Aust. Zool.* **13** : 259–298.

Gurney, R. 1924. The zoea of *Eurynome aspera*. *J. mar. biol. Ass. U.K.* **13** : 433–436.

Hansen, H. J. 1908. Crustacea Malacostraca. I. In: *The Danish Ingolf-Expedition* **3** 2 : 1–122. Copenhagen.

Hart, J. F. 1960. The larval development of British Columbia Brachyura. 2. Majidae, subfamily Oregoniinae. *Can. J. Zool.* **38** : 539–546.

Hartnoll, R. G. 1961. A re-examination of the spider crab, *Eurynome* Leach from British waters. *Crustaceana* **2** : 171–182.

—— 1964. The zoeal stages of the spider crab *Microphrys bicornutus* (Latr.). *Ann. Mag. nat. Hist.* (13) **7** : 241–246.

Haynes, E. 1973. Descriptions of prezoeae and stage I zoeae of *Chionoecetes bairdi* and *C. opilio* (Oxyrhyncha, Oregoniinae). *Fishery Bull. natn. ocean. atmos. Adm.* **71** : 769–775.

Heegaard, P. 1963. Decapod larvae from the Gulf of Napoli, hatched in captivity. *Vidensk. Meddr dansk naturh. Foren.* **125** : 449–493.

Ingle, R. W. 1977. The larval and post-larval development of the scorpion spider crab, *Inachus dorsettensis* (Pennant) (Family : Majidae), reared in the laboratory. *Bull. Br. Mus. nat. Hist.* (Zool.) **30** : 331–348.

—— **& Clark, P. F.** 1977. A laboratory module for rearing crab larvae. *Crustaceana* **32** : 220–222.

Italo Campodonico, G. & Leonardo Guzman, M. 1972. Desarrollo larval de *Eurypodius latreillei* Guerin en condiciones de laboratorio. (Crustacea Brachyura : Majidae, Inachinae). *An. Inst. Patagonia* **3** : 233–247.

Ito, K. 1968. Observations on the primary features of the newly hatched zoeal larvae of the zuwai-crab. *Bull. Japan sea reg. Fish. Res. Lab.* **20** : 91–93 (in Japanese).

Iwata, F. 1970. Studies on the development of the crab *Pugettia quadridens* (de Haan): I. Hatching and zoeae. *Publs Seto mar. biol. Lab.* **18** : 189–197.

Jewett, S. C. & Haight, R. E. 1977. Description of megalopa of snow crab *Chionoecetes bairdi* (Majidae, subfamily Oregoniinae). *Fishery Bull. natn. ocean. atmos. Adm.* **75** : 459–463.

Johns, D. M. & Lang, W. H. 1977. Larval development of the spider crab, *Libinia emarginata* (Majidae). *Fishery Bull. natn. ocean. atmos. Adm.* **75** : 831–841.

Kinahan, J. R. 1958. Remarks on the zoe of *Eurynome aspera*, and the habits of the animal in confinement. *Ann. Mag. nat. Hist.* **1** : 233–235.

—— 1860. Remarks on the zoe of *Eurynome aspera*, and the habits of the animal in confinement. *Proc. nat. Hist. Soc. Dublin* **2** : 77–79.

Kon, T. 1967. Fisheries biology of the Tanner crab, *Chionocetes opilio* – I. On the prezoeal larva. *Bull. Jap. Soc. scient. Fish.* **33** : 726–730.

Kuarata, H. 1963. Larvae of Decapod Crustacea of Hokkaido. 2. Majidae (Pisinae). *Bull. Hokkaido reg. Fish. Res. Lab.* **27** : 25–31.

—— 1969. Larvae of decapod Brachyura of Arasaki, Sagami Bay. IV. Majidae. *Bull. Tokai Reg. Fish. Res. Lab.* **57** : 81–127.

Kuwatani, Y., Wakui, T. & Nakanishi, T. 1971. Studies on the larvae and post-larvae of a Tanner crab, *Chionoecetes opilio elongatus* Rathbun. *Bull. Hokkaido reg. Fish. Res. Lab.* **37** : 32–40.

—— —— —— 1973. Studies on the larvae and post-larvae of a Tanner Crab, *Chionoecetes opilio elongatus* Rathbun. A correction to previous report (1971) on the external features of protozoeal larva. *Bull. Hokkaido reg. Fish. Res. Lab.* **39** : 93–94.

Lebour, M. V. 1927. Studies of the Plymouth Brachyura. I. The rearing of crabs in captivity with a description of the larval stages of *Inachus dorsettensis*, *Macropodia longirostris* and *Maia squinado*. *J. mar. Biol. Ass. U.K.* **14** : 795–820.

—— 1928. The larval stages of the Plymouth Brachyura. *Proc. zool. Soc. Lond.* (1928) : 473–560.

—— 1931. Further notes on larval Brachyura. *Proc. zool. Soc. Lond.* (1931) : 93–96.

—— 1944. Larval crabs from Bermuda. *Zoologica* **20** : 113–128.

Lo Bianco, S. 1904. Pelagische Tiefseefischerei der 'Maja' in der umgebung von Capri. *Beitrage zur Kenntnis des Meeres und seiner Bewohner*. Erster Band i-vi + 92 pp., Jena.

Motoh, H. 1970. Spec. Publs Pref. mar. Cult. Sta. Ishikawa 7–11 (not seen).

—— 1973. Laboratory-reared zoeae and megalopae of zuwai crab from the Sea of Japan. *Bull. Jap. Soc. scient. Fish.* **39** : 1223–1230.

—— 1976. The larval stages of Benizuwai-gani, *Chionoecetes japonicus* Rathbun reared in the laboratory. *Bull. Jap. Soc. scient. Fish.* **42** : 533–542.

Provenzano, A. J. & Brownell, W. N. 1977. Larval and early post-larval stages of the West Indian spider crab, *Mithrax spinosissimus* (Lamarck) (Decapoda : Majidae). *Proc. biol. Soc. Wash.* **90** : 735–752.

Rathbun, M. J. 1914. Stalk-eyed crustaceans collected at the Monte Bello Islands. *Proc. zool. Soc. Lond.* (1914) : 653–664.

—— 1923. The brachyuran crabs collected by the U.S. Fisheries Steamer 'Albatross' in 1911, chiefly on the west coast of Mexico. *Bull. Am. Mus. nat. Hist.* **48** : 619–637.

Rice, A. L. & Ingle, R. W. 1975. The larval development of *Carcinus maenas* (L.) and *C. mediterraneus* Czerniavsky (Crustacea, Brachyura, Portunidae) reared in the laboratory. *Bull. Br. Mus. nat. Hist.* (Zool.) **28** : 101–119.

—— **& Williamson, D. I.** 1977. Plaoktonic stages of Crustacea Malacostraca from Atlantic Seamounts. '*Meteor' Forsch.-Ergenb.*, D **26** : 28–64.

Sandifer, P. A. & van Engel, W. A. 1971. Larval development of the spider crab, *Libinia dubia* H. Milne Edwards (Brachyura, Majidae, Pisinae), reared in laboratory culture. *Chesapeake Sci.* **12** : 18–25.

—— —— 1972. Larval stages of the spider crab, *Anasimus latus* Rathbun, 1894 (Brachyura, Majidae, Inachinae) obtained in the laboratory. *Crustaceana* **23** : 141–151.

Schlegel, C. 1911. Sur le developpement de *Maia squinado* Latr. *C. r. hebd. Seanc. Acad. Sci. Paris* **153** : 480–482.

Steedman, H. F. 1976. General and applied data on formaldehyde fixation and preservation of marine zooplankton (pp. 103–154). In: **Steedman, H. F.** (ed.), *Zooplankton fixation and preservation. Monographs on oceanographic methodology.* UNESCO Press. 350 pp. Paris.

Stephenson, K. 1912. Report on the Malacostraca collected by the 'Tjalfe'-Expedition, under the direction of cand. mag. Ad. S. Jensen, especially at W. Greenland. *Vidensk. Meddr. dansk naturh. Foren.* **64** : 57–134.

—— 1917. Zoogeographical investigation of certain fjords in southern Greenland, with special reference to Crustacea, Pycnogonida and Echinodermata, including a list of Alcyonaria and Pisces. *Meddr Grønland* **53** : 231–378.

—— 1935. Crustacea Decapoda. The Godthaab Expedition 1928. *Meddr Grønland* **80** : 1–94.

Tanase, H. 1967. Preliminary note on zoea and megalopa of the giant spider crab, *Macrocheira kaempferi* de Haan. *Publs Seto mar. biol. Lab.* **15** : 303–309.

Thompson, J. V. 1836. On the double metamorphosis in *Macropodia phalangium*, or spider crab; with proofs of the larvae being zoea in Gegarcinus hydrodromus, Thelphusa erythropus, Eriphia carribaea, and Grapsus pelagicus. *Ent. Mag.* **3** : 370–375.

Thomson, C. W. 1874. The Depths of the Sea. i-xvi + 527 pp. London.

Williamson, H. C. 1911. Report on the larval and later stages of *Portunus holsatus*, Fabr., *Portunus puber*, L; *Portunus depurator*, Leach; *Hyas araneus* (L.); *Eupagurus bernhardus* L; *Galathea dispersa*, Spence Bate; *Crangon trispinosus* (Hailstone); *Cancer pagurus*, L. *Scient. Invest. Fishery Bd Scotl.* (1909) : 1–20.

—— 1915. Crustacea Decapoda larven. *Nord. Plankt.* **18** : 315–588.

Yang, W. T. 1967. A study of zoeal, megalopal, and early crab stages of some oxyrhynchous crabs (Crustacea: Decapoda). Doctoral Dissertation, University of Miami.

—— 1968. The zoeae, megalopa, and first crab of *Epialtus dilatatus* (Brachyura, Majidae), reared in the laboratory. *Crustaceana* (Suppl.) **2** : 181–202.

—— 1976. Studies on the western Atlantic Arrow crab Genus *Stenorhynchus* (Decapoda Brachyura, Majidae). I. Larval characters of two species and comparison with other larvae of Inachinae). *Crustaceana* **31** : 157–177.

Manuscript accepted for publication 16 November 1978

On the spider genus *Cynapes* (Araneae : Salticidae)

F. R. Wanless

Department of Zoology, British Museum (Natural History), Cromwell Road, London SW7 5BD

Introduction

The genus *Cynapes* Simon, 1900 at present includes two known species, the type species *Cynapes wrightii* (Blackwall) from the Seychelles and *C. baptizatus* (Butler) from Rodriguez. Two species previously included in the genus are removed elsewhere: *C. albolineatus* (Peckham & Peckham) from Madagascar is returned to *Bavia* Simon, 1877, the genus in which it was originally described, while *C. canosus* Simon from Mauritius is transferred into *Marengo* Peckham & Peckham, 1892 .

Cynapes baptizatus and *Marengo canosa* comb. nov. are described below. *C. wrightii* has not been included because it has recently been described elsewhere (Wanless, in press). *Bavia albolineata* comb. rev. will be dealt with when *Bavia* is revised as preliminary observations suggest that this placement is doubtful, unfortunately I am unable to propose a more satisfactory solution at the present time.

Wanless (in press) has suggested that *Cynapes* may be synonymous with *Baviola* Simon, 1897. The structure of the genitalia shows that the genera are closely related, but they can be separated by the shape of the carapace and eye formula. These latter characters were extensively used by early salticid workers for defining genera and the failure to consider genitalic characters has largely resulted in the present unsatisfactory taxomony of the family. Somatic characters can nevertheless provide evidence of relationships particularly in cases when the genitalia are relatively simple and of similar forms. For the present, *Cynapes* is therefore considered to be a valid genus, but it may ultimately be synonymized with *Baviola* or, as seems more likely, be given a subgeneric rank. Subgenera have not often been used in this family and they cannot for the moment be justified as too many tropical Salticidae are poorly known, and it is impossible to present an overall view of the relationships.

Genus ***CYNAPES*** Simon

Cynapes Simon 1900 : 393. Type species *Salticus wrightii* Blackwall, by original designation. Simon, 1901 : 462, 467, 469, 471. Petrunkevitch, 1928 : 186. Bonnet, 1956 : 1334. Wanless (in press).

DEFINITION. Medium to large spiders ranging from about 5·0 to 8·0 mm in length. Species sexually dimorphic. Distinctive colour markings present, not hirsute. Legs I heaviest especially in females. *Carapace*: longer than broad, moderately low with convex lateral margins; fovea in shallow depression behind PL. *Eyes*: anteriors subcontiguous, apices more or less level or slightly recurved; posterior median eyes small, slightly closer to AL than to PL; posterior and anterior rows subequal in width; quadrangle length between 40 and 50 per cent of carapace length. *Clypeus*: low. *Chelicerae*: robust, moderately porrect, sometimes with an apophysis on anterior surface; promargin with 3 or 4 teeth, retromargin with 6 or 7. *Maxillae*: moderately elongate, parallel or slightly convergent. *Labium*: elongate tongue-shaped. *Sternum*: scutiform to elongate scutiform, sometimes slightly narrowed anteriorly. *Abdomen*: elongate with a pattern; spinnerets closely grouped, posteriors slightly longer than the rest, anteriors more robust; tracheal spiracle a transverse slit just in front of the anterior spinnerets or positioned midway between the middle of the abdomen and the anterior spinnerets (internal system not examined). *Legs*: legs I heaviest, sometimes with scanty ventral fringes; not scopulate, spines numerous and strong on legs I–II but fewer and weaker on legs III–IV. *Epigyne*: simple and of similar forms; orifice

Bull. Br. Mus. nat. Hist. (Zool.) **37** (1) : 67–72

Issued 29 November 1979

rounded with obscure lateral openings leading to convoluted fertilization ducts. *Female palp*: long and slender, clothed in hairs. *Male palp*: simple, of variable form; tegulum with distal coiled or partly coiled embolus; tibial apophysis slender, unmodified.

DIAGNOSIS AND AFFINITIES. *Cynapes* is closely related to *Baviola*, but may be distinguished by the low carapace and the presence of a broad space between the posterior lateral eyes and carapace margin; the space being much greater than the diameter of the posterior eye.

List of species in the genus *Cynapes* Simon, 1900
Cynapes wrightii (Blackwall, 1877)
C. baptizatus (Butler, 1876)

Cynapes baptizatus (Butler)

(Fig. 1A–K)

Salticus baptizatus Butler, 1876 : 440, ♀. Holotype ♀, Rodriguez (BMNH.1876.13) [Examined]. Butler 1879 : 501, 507, 509, pl. LII.

Cynapes baptizatus: Simon, 1901 : 467. Roewer, 1954 : 980. Bonnet, 1956 : 1335. Prószyński, 1971: 395. Wanless (in press).

DIAGNOSIS. *C. baptizatus* can be readily distinguished from *C. wrightii*, the only other species in the genus, by having the tracheal slit positioned just in front of the anterior spinnerets. In *C. wrightii* the slit is clearly positioned a short distance away from the spinnerets, with the intervening space clothed in short hairs.

MALE FROM RODRIGUEZ (previously undescribed). *Carapace* (Fig. 1E): orange-brown with faint sooty markings, foveal region and posterior half of quadrangle pale yellow; from below AL to posterior lateral margin a white haired band with scattered white hairs in pale yellow areas (mostly rubbed in specimens at hand). *Eyes*: with black surrounds; anteriors subcontiguous with apices more or less level, fringed in white hairs. *Clypeus*: white haired. *Chelicerae* (Fig. 1F): with frontal apophyses; orange-brown; promargin with 3 teeth, retromargin with 6. *Maxillae and labium*: orange-brown. *Sternum* (Fig. 1G): pale yellow. *Abdomen*: pale yellow with black bands above and blackish lateral markings, venter light yellow tinged black; spinnerets whitish yellow. *Legs*: legs I heaviest, tarsi pale yellow, other segments yellow-brown to orange-brown tinged black with scanty ventral white haired fringes on tibiae and patellae; other legs pale yellow. Spination of legs I: metatarsi with 2 pairs of ventral spines, tibiae with 3 pairs, patellae with 1 spine, femora with 2 dorsal and 2 prolaterals. *Palp* (Fig. 1C, H): yellow-orange heavily blackened, but cymbium white tipped.

Dimensions (mm): total length 5·68; carapace length 2·36, breadth 2·06; abdomen length 3·36; eyes, anterior row 1·6, middle row 1·38, posterior row 1·64; quadrangle length 1·08. *Ratios*: AM : AL : PM : PL :: 12·5 : 7 : 1·1 : 6; AL–PM–PL :: 7–9.

FEMALE FROM RODRIGUEZ. Body form and colour markings (Fig. 1A, D), more or less as in ♂, except for the following: *Chelicerae*: lacking apophyses; promargin with 4 teeth, retromargin with 6. *Sternum* (Fig. 1I): more attenuate in front (to allow for the heavier coxae I). *Legs*: legs I massive; spines: metatarsi with 2 ventral pairs, tibiae with 3, on both segments prolateral spines rather small, patellae with 1 spine, femora with 3 dorsal and 2 distal prolaterals; other leg spines few and generally weak. *Palps*: light yellow. *Epigyne* (Fig. 1J, K): pale with indistinct circular orifice and posterior fertilization ducts.

Dimensions (mm): total length 8·16; carapace length 3·44, breadth 2·96; abdomen length 5·0; eyes, anterior row 2·10, middle row 1·88, posterior row 2·2; quadrangle length 1·44. *Ratios*: AM : AL : PM : PL :: 16 : 8 : 1·5 : 7; AL–PM–PL :: 9–13.

VARIATION. Another male measures 5·0 mm total length, 2·60 mm carapace length. Females vary from 6·5 to 8·1 mm total length, 2·7 to 2·96 mm carapace length (5 specimens). The conformation of the fertilization ducts is inconsistent, but the general appearance of the epigynes does not show much variation. Some individuals are paler, probably as a result of long preservation.

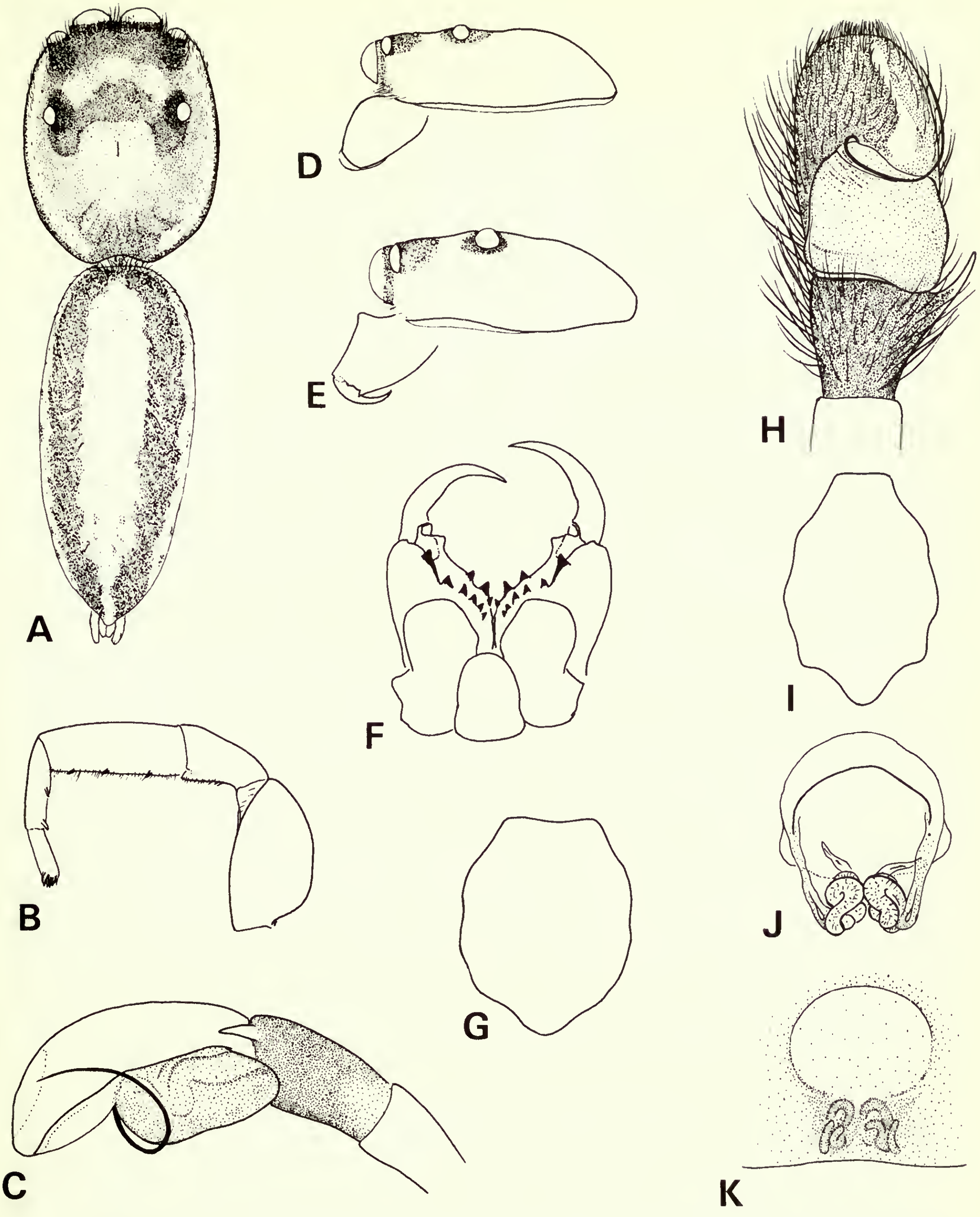


Fig. 1 *Cynapes baptizatus*, ♂: C, palp, lateral view; E, carapace, lateral view; F, chelicerae; G, sternum; H, palp, ventral view. ♀: A, dorsal view; B, leg I; D, carapace, lateral view; I, sternum; J, vulva; K, epigyne.

DISTRIBUTION. Rodriguez.

MATERIAL EXAMINED. Holotype ♀, Rodriguez, Transit of Venus Exped., 1874–75, (*G. Gulliver*) (BMNH.1876.13). RODRIGUEZ: x. 1918, 2. ♂♂, 5 ♀♀ (*H. P. Thomasset & H. J. Snell*) (BMNH. 1952.3.6.95–104).

Marengo canosa (Simon) comb. nov.

(Fig. 2A-K)

Cynapes canosa Simon, 1900 : 393, ♂, ♀. LECTOTYPE ♂, PARALECTOTYPE ♀ (here designated) Mauritius (MNHN, Paris, no. 20353) [Examined]. Simon, 1901 : 462, 463, 467. Roewer, 1954 : 980. Bonnet, 1956 : 1335. Prószyński, 1971 : 396.

The female here designated paralectotype is smaller than the lectotype male and as such does not agree with the original description (Simon, 1900). However, as the remaining data are in agreement it is assumed that Simon's measurement is erroneous, and that the specimens are syntypes.

AFFINITIES AND DIAGNOSIS. Uncertainties as to the affinities of this species arise from the suspicion that the specimens described below may not be conspecific, principally because of differences in the position of the posterior lateral eyes in relation to the carapace width (Fig. 2A, G). The structure of the genitalia is in broad agreement with the genus as defined in Wanless (1978). However, legs I are not grossly enlarged, the chelicerae are not set well back and, furthermore, in the male they are moderately porrect with low lateral keels. These characters serve to distinguish *M. canosa* from all other known species of *Marengo*, but the generic placement will have to be reconsidered when more is known of tropical salticids.

MALE LECTOTYPE. *Carapace* (Fig. 2A, B): Dark reddish brown with an iridescent sheen in eye area; clothed with short scattered white hairs forming an obscure band encircling eye region, fovea lacking. *Eyes*: with black surrounds; anteriors subcontiguous with apices slightly recurved; fringed in white hairs. *Clypeus*: low; orange-brown edged black with scattered light brown hairs. *Chelicerae* (Fig. 2I): dark orange, shiny, lateral margins black forming slightly raised keels; promargin with 3 teeth, retromargin with 6 followed by a blunt apophysis. *Maxillae*: brown. *Labium*: brown with blackish lateral depressions. *Sternum* (Fig. 2F): orange-brown. *Abdomen*: yellow-brown lightly mottled black with a dark reddish brown scutum sparsely clothed in fine silky white hairs (mostly rubbed). *Legs*: legs I heaviest, dark orange-brown with scanty ventral fringes on tibiae and patellae; other legs yellow-brown to light orange-brown. Spination of legs I: metatarsi with 2 pairs of stumpy spines; tibiae with 3 distal pairs of normal spines, but proximal pair offset; patellae with 1 spine; femora with 3 distal dorsal and 2 prolateral spines. Other leg spines weaker and fewer especially on legs III–IV. *Palp* (Fig. 2D, E): orange-brown; embolus apparently with 3 spirals.

Dimensions (mm): total length 5·16; carapace length 2·4, breadth 2·16; abdomen length 2·84; eyes, anterior row 1·64, middle row 1·58, posterior row 1·84; quadrangle length 1·04. *Ratios*: AM : AL : PM : PL :: 12 : 7 : 1·2 : 6·3; AL–PM–PL :: 7–8.

FEMALE PARALECTOTYPE. *Carapace* (Fig. 2G): dark reddish brown, weakly iridescent in eye region; thinly clothed in short whitish hairs; fovea lacking. *Eyes*: with black surrounds; anteriors subcontiguous, apices more or less level, fringed in white hairs. *Clypeus*: low; orange edged black, sparsely white haired. *Chelicerae* (Fig. 2H): finely rugose; yellow-orange, weakly iridescent; promargin with 3 teeth, retromargin with 5. *Maxillae*: brownish orange. *Labium*: blackish tipped brownish orange. *Sternum*: orange-brown tinged black. *Abdomen*: pale yellow-brown with faint blackish mottling; spinnerets blackish. *Legs*: legs I only slightly heavier than the rest. Yellow-brown. Spination of legs I: metatarsi with 2 pairs of ventral spines; tibiae with 3 pairs; patellae with 1 spine; femora with 3 dorsals and 1 prolateral. Other leg spines generally weak and fewer except for the femoral spines. *Palp*: yellow-brown. *Epigyne* (Fig. 2K): vulva not examined.

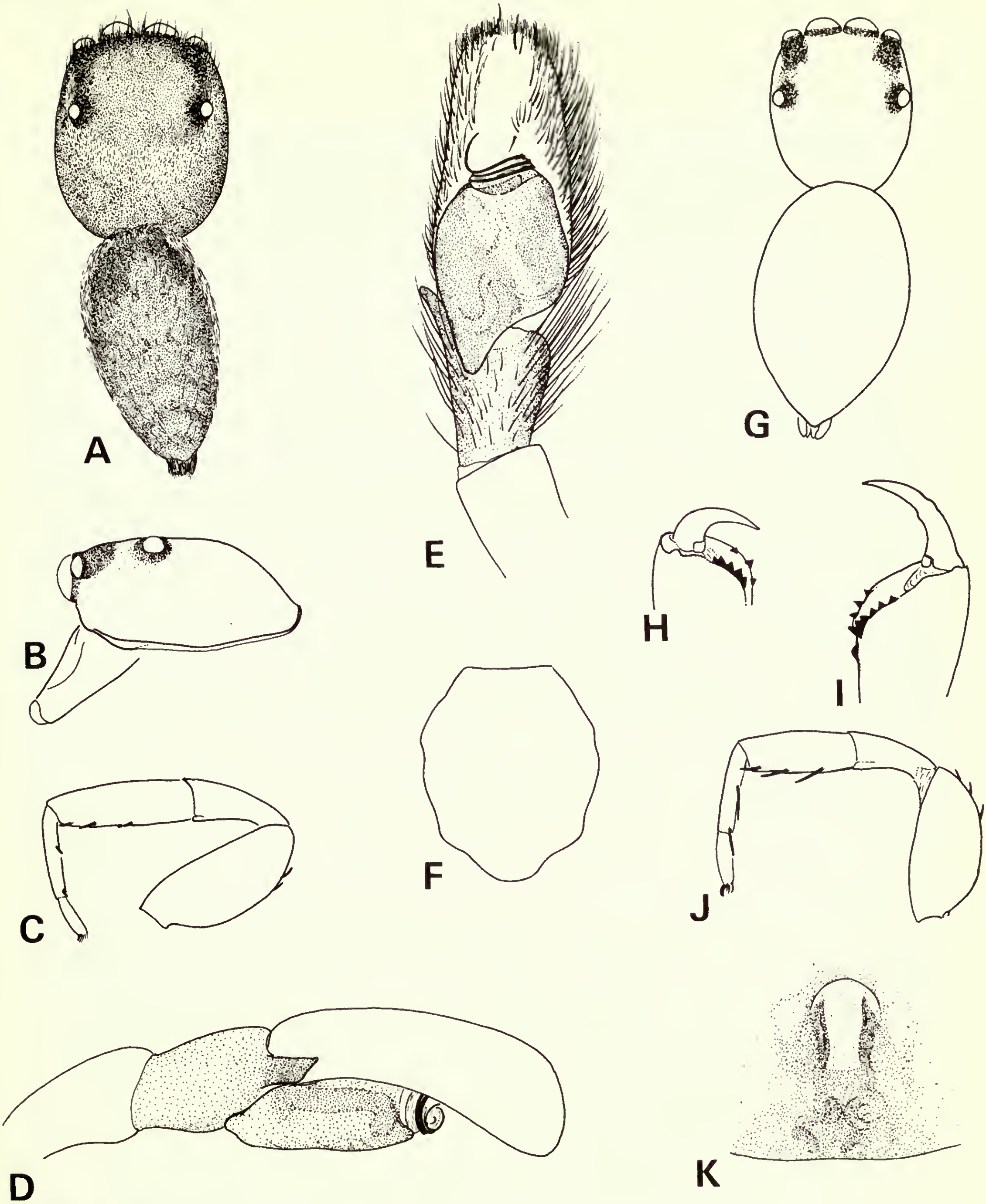


Fig. 2 *Marengo canosa*, lectotype ♂: A, dorsal view; B, carapace, lateral view; C, leg I; D, palp, lateral view; E, palp, ventral view; F, sternum; I, chelicera. Paralectotype ♀: G, dorsal view; H, chelicera; J, leg I; K, epigyne.

Dimensions (mm): total length 4·36; carapace length 1·78, breadth 1·54; abdomen length 2·72; eyes, anterior row 1·36, middle row 1·28, posterior row 1·52; quadrangle length 0·84. *Ratios*: AM : AL : PM : PL :: 10 : 6 : 1·1 : 5; AL–PM–PL :: 6–6·5.

VARIATION. Unknown.

DISTRIBUTION. Mauritius.

MATERIAL EXAMINED. Lectotype ♂, paralectotype ♀, Mauritius (*Ch. Alluaud*) (MNHN, Paris, no. 20353).

Acknowledgments

I wish to thank M. M. Hubert, Muséum National d'Histoire Naturelle, Paris, for the loan of specimens and Mr D. Macfarlane, Commonwealth Institute of Entomology, London, for reading the manuscript.

References

Blackwall, J. 1877. A list of spiders captured in the Seychelles Islands by Professor E. Perceval Wright, M.D., F.L.S. with descriptions of species supposed to be new to arachnologists. *Proc. R. Ir. Acad.* **3** : 1–22.

Bonnet, P. 1945–61. *Bibliographia Araneorum* 3 vols. Imprimerie Douladoure, Toulouse.

Butler, A. G. 1876. Preliminary notice of new species of Arachnida and Myriapoda from Rodriguez collected by Messrs George Gulliver and H. H. Slater. *Ann. Mag. nat. Hist.* (4) **17** : 439–446.

—— 1879. Myriopoda and Arachnida. (in) Zoology of Rodriguez. An account of the petrological, botanical and zoological collections made in Kerguelen's Land and Rodriguez during the Transit of Venus Expeditions, carried out by order of Her Majesty's Government in the years 1874–75. *Phil. Trans. R. Soc.* **168** : 497–509.

Peckham, G. W. & Peckham, E. G. 1892. Ant-like spiders of the family Attidae. *Occ. Pap. Wis. nat. Hist. Soc.* **2** (1) : 1–83.

Petrunkevitch, A. 1928. Systema Aranearum. *Trans. Conn. Acad. Arts Sci.* **29** : 1–270.

Prószyński, J. 1971. Catalogue of Salticidae (Aranei) specimens kept in major collections of the world. *Annls zool. Warsz.* **28** : 367–519.

Roewer, C. F. 1954. *Katalog der Araneae.* **2**, Abt. B : 924–1290. Institut Royal des Sciences Naturelle de Belgique, Bruxelles.

Simon, E. 1877. Études arachnologiques 19e Mémoire. XXVII: Arachnides recueillis à Assinie (Afrique occidentale) par MM. Chaper et Alluaud. *Annls Soc. ent. Fr.* (6) **7** : 261–276.

—— 1897. Études arachnologiques 29e Mémoire (1) XLVI. Arachnides recueillis en 1895 par M. le Dr A. Brauer (de l'Université de Marburg) aux îles Séchelles. *Annls Soc. ent. Fr.* **66** : 370–388.

—— 1900. Descriptions d'arachnides nouveaux de la famille des Attidae. *Annls Soc. ent. Belg.* **44** : 381–407.

—— 1901. *Histoire Naturelle des Araignées*, **2** (3) : 381–668. Paris, Roret: Libraire Encyclopédique.

Wanless, F. R. 1978. A revision of the spider genus *Marengo* (Araneae : Salticidae). *Bull. Br. Mus. nat. Hist.* (Zool.) **33** (4) : 231–296.

—— (in press). The salticid spiders (Araneae : Salticidae) of the Seychelles. *Revue zool. afr.*

Manuscript accepted for publication 22 January 1979

A new species of *Phthiracarus* (Acari, Cryptostigmata) from Austria

B. W. Parry

Department of Zoology, British Museum (Natural History), Cromwell Road, London SW7 5BD

Introduction

A small collection of mites from oak litter in the Vienna Woods, Austria was examined by Sheals in connection with a computer study of phenetic affinity within the Phthiracaroidea (Sheals, 1969). The material was found to contain several specimens of an undescribed phthiracarid mite, the notogastral integument of which was particularly striking and apparently unique amongst the known members of the superfamily. Moreover, although the species showed an overall similarity to *Steganacarus*, its anal chaetotactic pattern corresponded to that of *Phthiracarus*. Classification of the mite was deferred at this time and Sheals excluded it from his study. However, in view of its interesting morphological features a detailed description was considered desirable and is given below, based on the seven available specimens.

Family **PHTHIRACARIDAE** Perty, 1841

Phthiracarus papillosus sp. nov.

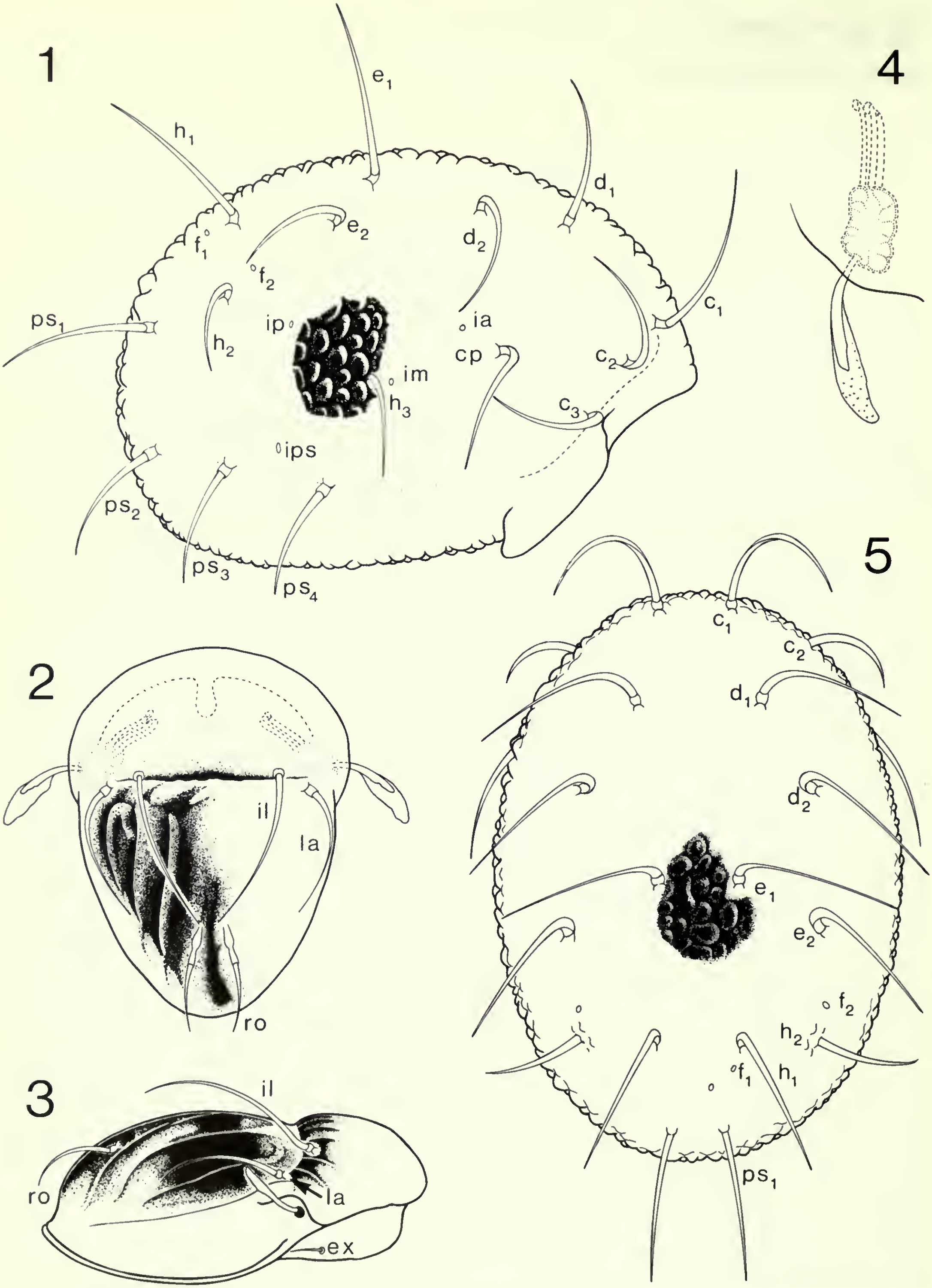
Aspis (Figs 2–4; Pl. 1b): 242–282 µm long and with a greatest width of 181–212 µm. All the dorsal setae are rather long, stout and procumbent. The interlamellar setae (*il*) are about 1·5 times the length of the lamellars (*la*) and extend two-thirds of the distance between the bases of the interlamellar and rostral setae (*ro*). The latter almost reach the anterior aspal margin. The sensilli are 40–55 µm long, lanceolate and striated. Three finger-like tracheoles are associated with each bothridium and there is a single pair of short exobothridial setae (*ex*). In front of the *il–la* setae there is a pronounced median keel and on each side three lateral keels arranged in an oblique row (Pl. 1b). Of the lateral keels, the paraxial pair is the longest and the antiaxial pair the shortest. The prodorsal integument is not strongly ornamented and appears to be finely punctate as in other *Phthiracarus* species. Behind the sensilli the integument is raised into a number of low longitudinal ridges.

Notogaster (Figs 1, 5; Pls la; 2d): 464–606 µm in length along a line through c_1–h_1, and with a greatest depth of 333–484 µm. All the setae are stout, slightly recurved and more or less equal to the distance c_1–d_1 (Pl. 1a). Seta c_3 is inserted on the posterior margin of the collar and setae c_{1-2} submarginally. Vestigial f_1 is located just below the seta h_1. The fissures *ip* and *ips* are present. In one paratype *ip* and *ips* were only present on one side. The integument is densely and irregularly papillate (Pl. 2d).

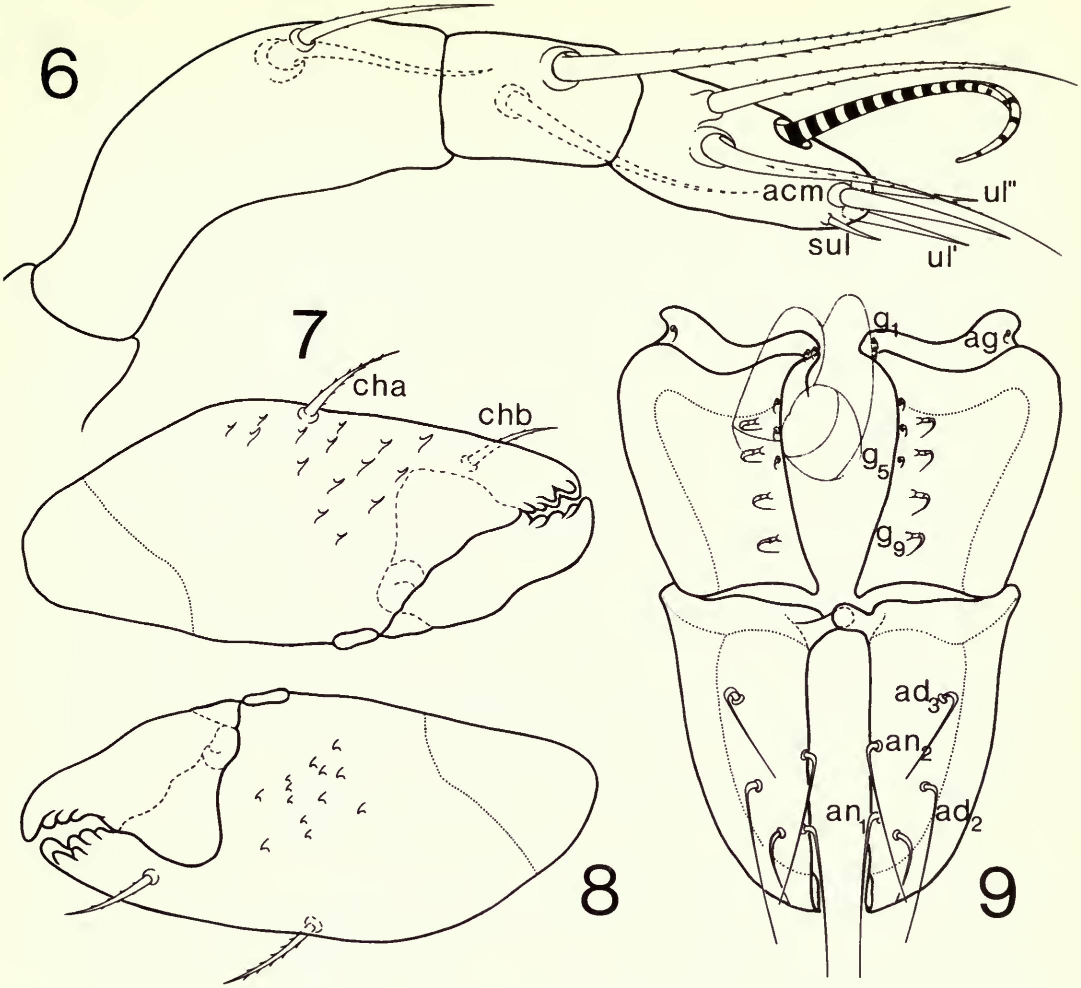
Ano-genital region (Fig. 9; Pl. 1f): There are two pairs of comparatively long anal setae (an_{1-2}) located marginally and three pairs of adanals (ad_{1-3}) forming an oblique row submarginally, the longest in the row being ad_2 which is approximately equal in length to the anal setae. Scanning electron micrographs show that all the setae on the anal plates are weakly serrated. On each genital plate there are nine simple genital setae arranged in two rows. Setae g_{1-5} are minute and located on the paraxial border while the other four pairs (g_{6-9}) are moderately short and submarginal. A single aggenital seta *ag* is located antiaxially in the genital furrow. The integument of the genital and anal plates is weakly papillate (Pl. 1f) with the exception of the areas bearing setae (an_{1-2}) where the integument has no distinct ornamentation. There are three pairs of genital papillae, the anterior pair being rather small.

Bull. Br. Mus. nat. Hist. (Zool.) **37** (1) : 73–79

Issued 29 November 1979


1
e_1
h_1
d_1
e_2
f_1
d_2
f_2
c_1
ps_1
ip
ia
h_2
cp
c_2
im
h_3
c_3
ips
ps_2
ps_3
ps_4
4
2
il
la
ro
5
c_1
c_2
d_1
d_2
e_1
e_2
f_2
h_2
f_1
h_1
ps_1
3
il
ro
la
ex

Figs 1–5 *Phthiracarus papillosus:* (1) notogaster, lateral; (2) aspis, dorsal; (3) aspis, lateral; (4) sensillus and bothridium; (5) notogaster, dorsal.



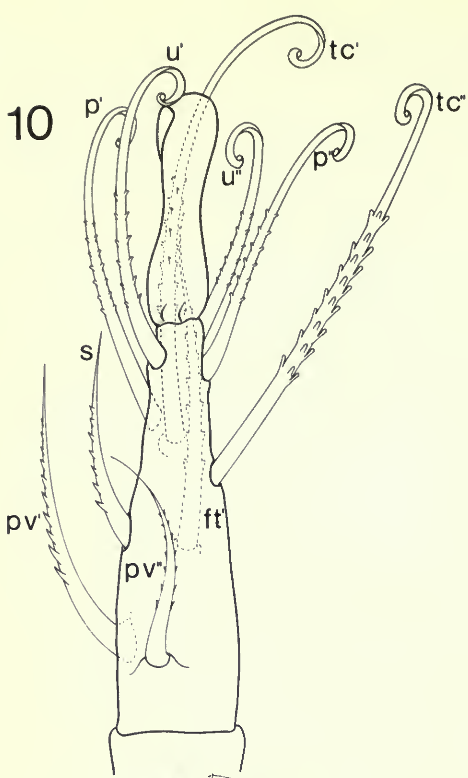
Figs 6–9 *Phthiracarus papillosus:* (6) pedipalp; (7) chelicera, paraxial; (8) chelicera, antiaxial; (9) ano-genital region.

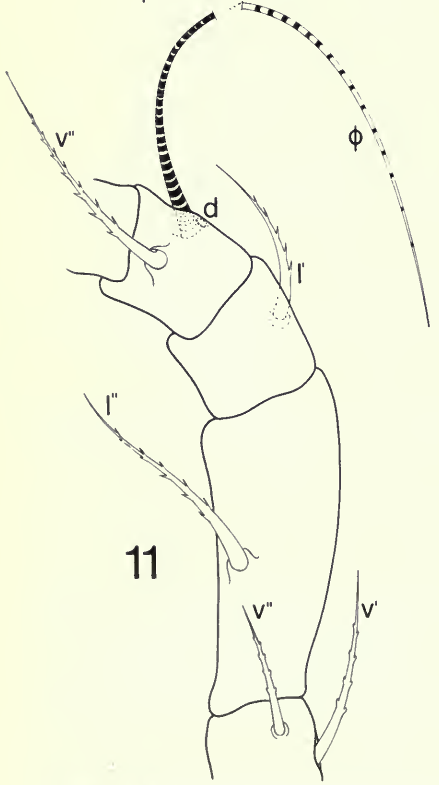
Infracapitulum: This is typically phthiracaroid in form (see for example, Parry, 1979). Of the three pairs of adoral setae, the anterior pair are brush-like distally and the two posterior pairs weakly serrated.

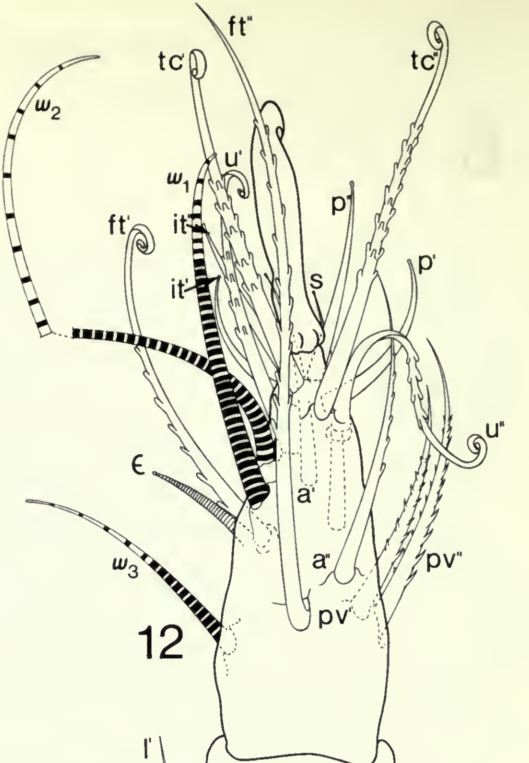
Pedipalps (Fig. 6): Three-segmented with the setal formula (2–2–7). Four of the tarsal setae (*acm*, *ul'*, *ul''* and *sul*) are eupathidial, *sul* being rather short.

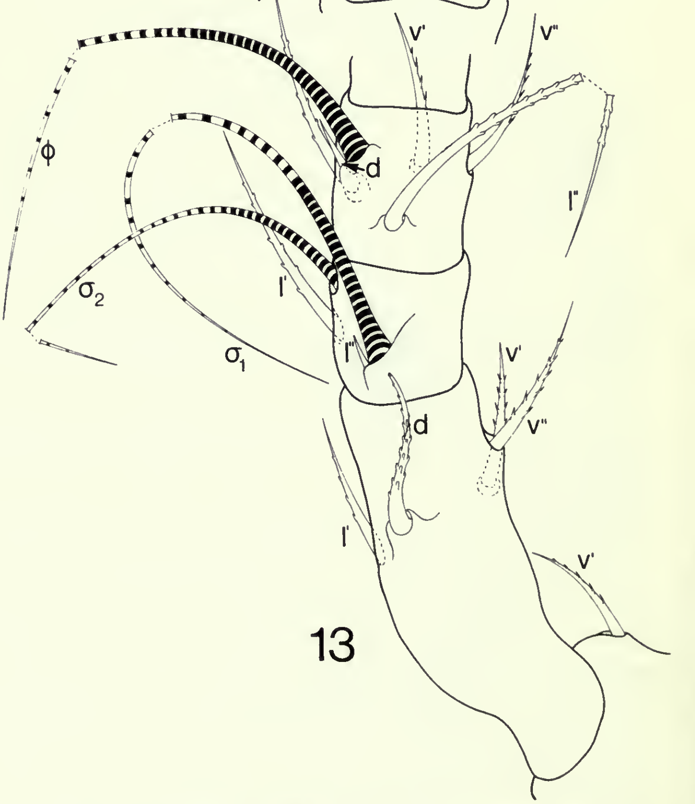
Chelicerae (Figs 7, 8): The movable digit has four teeth and the fixed digit carries five. The latter are arranged in two rows, an outer one of two teeth and an inner row of three. The principal segment carries 12–21 sharply pointed spines on the paraxial surface and 13–26 conical spines antiaxially. Although cheliceral spines have been observed in other species of *Phthiracarus* (see Parry, 1979), the greatest number has always been observed on the paraxial surface. Setae *cha* and *chb* are both serrated, *cha* being somewhat longer than *chb*. The cheliceral integument is finely punctate.

Legs (Figs 10–13; Pl. 1c–e): The solenidial formulae for the legs are I (2–1–3); II (1–1–2); III (0–1–1) and IV (0–1–0). On tarsus I solenidion ω_2 is coupled with a small distal seta. The latter is conical in shape and apparently lacks the longitudinal constriction observed in certain other species of *Phthiracarus* (Parry, 1979) and *Steganacarus* (Parry, 1978). On tibia I the reduced


10
tc'
u'
p'
u''
p''
tc''
s
pv'
ft''
pv''




ft''
tc'
tc''
ω2
u'
ω1
it''
ft'
p''
it'
s
p'
ε
u''
a'
ω3
a''
pv''
pv'
12


v'
v''
φ
d
l''
σ2
l'
σ1
l''
v'
d
v''
l'
v'
13

Figs 10 & 11 *Phthiracarus papillosus*, posterolateral aspect of leg IV: (10) tarsus; (11) tibia to trochanter.

Figs 12 & 13 *Phthiracarus papillosus*, posterolateral aspect of leg I: (12) tarsus; (13) tibia to trochanter.

(Figs 10 and 12 are drawn at the same magnification.)

dorsal seta coupled with solenidion φ is rather long and prominent (Pl. 1e) but on tibiae II–IV it is much shorter. Solenidion σ_1 on genu I is coupled with a small posterolateral seta l''. The formulae for the leg setae are I (1–4–2–5–16–1); II (1–3–2–3–12–1); III (2–2–1–2–10–1) and IV (2–1–1–2–10–1). On all four tarsi the setal arrangement closely resembles that found in other species of the genus. On tarsus I six of the setae ((it), (p), s and a') are eupathidial and apparently blunt distally. The famulus ε is short, rugose and closely associated with ω_1. Seta ft' is somewhat unusual in being hooked distally (this seta is generally straight on all four tarsi in *Phthiracarus* species). Setae (tc) and (u) on tarsus I (Pl. 1c) and (tc), (u), (p) and s on tarsi II–IV are covered with whorls of rather blunt spicules in the middle third. On femur I seta d is thickened and densely serrated (Pl. 1d), the serrations being blunt distally (in other species of the genus the serrations are fewer and sharply pointed). All the tarsi terminate in a single claw bearing two ventral teeth and an antero- and posterolateral row of serrations.

MATERIAL: Holotype, BMNH reg. no. 1978.11.10.1, and six paratypes, BMNH reg. no. 1978. 11.10.2–7, from oak litter, Leopoldsberg, Austria. The material was collected by Professor W. Kühnelt, 4 July 1948 and 13 November 1948.

REMARKS: In relation to the general shape of the aspis and the integumental ornamentation of the notogaster, *P. papillosus* is atypical of the genus *Phthiracarus*, showing affinities with *Steganacarus* and *Tropacarus*. In these two genera the prodorsal integument posterior to the *il–la* setae is raised into a number of longitudinal ridges, while anteriorly there is a median keel and, in certain species, a pair of lateral keels. However, the presence of seven keels in *P. papillosus* is apparently unique in the Phthiracaridae. An ornamented notogastral integument is also present in *Tropacarus* and *Steganacarus*. In the former genus the integument may be described as being irregularly stellato-papillate (Pl. 2a, b) while in *Steganacarus*, although usually punctate (Pl. 2f), a rather striking ornamentation (raised reticulate) has been observed in *Steganacarus clavigerus*, a species described by Berlese (1904) from the Boboli Gardens, Italy (Pl. 2c). In addition, the notogastral setae of *P. papillosus* are rather long and stout as in *Steganacarus* species while the serrated nature of the setae in the ano-genital region is characteristic of both *Steganacarus* and *Tropacarus*.

Despite these affinities the Austrian species has been classified in *Phthiracarus*. Procumbent interlamellar setae and a 2+3 setal arrangement on the anal plates are sufficient to distinguish *Phthiracarus* from other phthiracarid genera. However, to accommodate *P. papillosus* in Parry's (1979) definition of the genus, the following modifications must be made: 'The integument of the dorsal and ventral shields is densely punctate *and/or papillate* while that of the infracapitulum, chelicerae and appendages is punctate.' ' . . . aspis *usually* without a median keel *or lateral keels*.' Although the integument of other *Phthiracarus* species appears smooth when seen with the light microscope, scanning electron micrographs have revealed that in a number of British species the integument of the genital plates is weakly papillate and punctate (Pl. 2e).

References

Parry, B. W. 1978. A new species of *Steganacarus* (Acari, Cryptostigmata) from Israel. *Bull. Br. Mus. nat. Hist.* (Zool.) **33** (4) : 279–285.

—— 1979. A revision of the British species of the genus *Phthiracarus* Perty, 1841 (Cryptostigmata : Euptyctima). *Bull. Br. Mus. nat. Hist.* (Zool.) **35** (5) : 323–363.

Sheals, J. G. 1969. Computers in acarine taxonomy. *Acarologia* **11** : 376–396.

Manuscript accepted for publication 11 December 1978

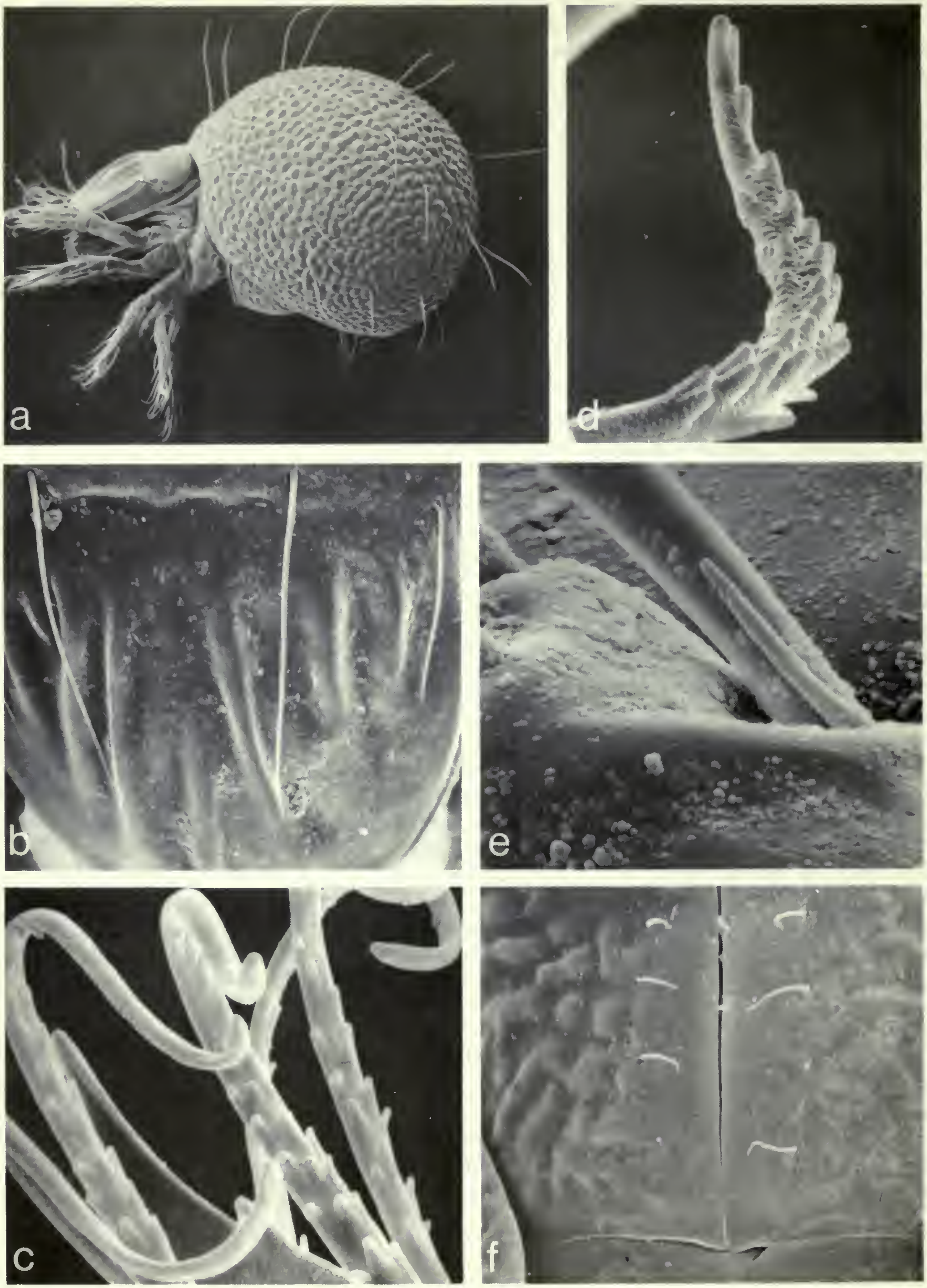


Plate 1 *Phthiracarus papillosus:* (a) lateral aspect, ×70; (b) aspis, dorsal aspect, ×400; (c) tectal and unguinial setae on tarsus I, ×3500; (d) dorsal seta on femur I, ×5000; (e) solenidion and associated seta on tibia I, dorsolateral aspect, ×3650; (f) genital plates, ×480.

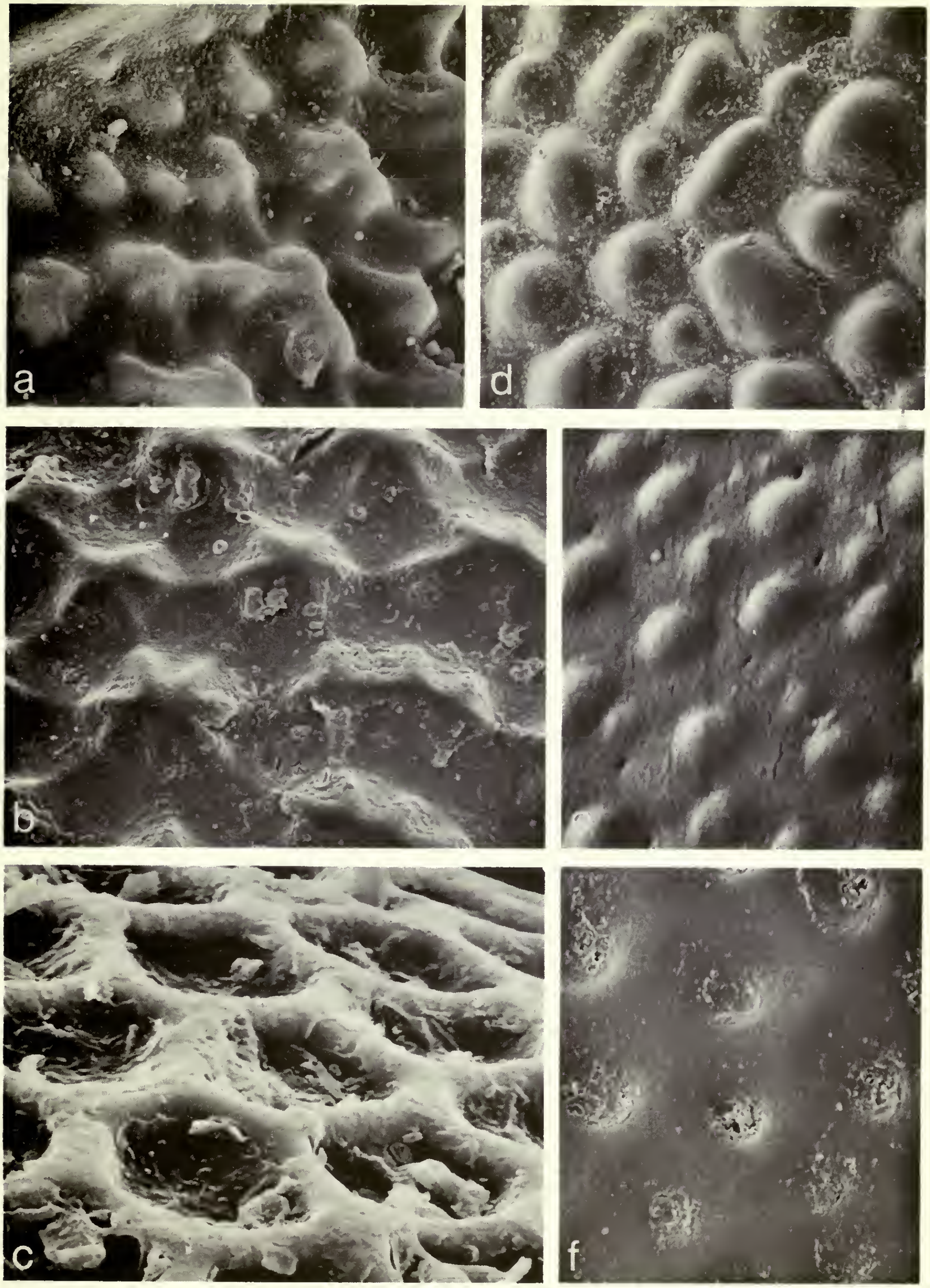


Plate 2 Integument: notogaster (a–d, f); genital plate (e). (a) *Tropacarus pulcherrimus* (Berlese), ×550. (b) *Tropacarus carinatus* (C. L. Koch), ×700. (c) *Steganacarus clavigerus* (Berlese), ×1800. (d) *Phthiracarus papillosus*, ×1100. (e) *Phthiracarus affinis* (Hull), ×8000. (f) *Steganacarus magnus* (Nicolet), × 700.

An Important New Title From British Museum (Natural History) Monographs

British Marine Amphipoda: Gammaridea

by R. J. Lincoln

1979 658pp 2,300 figures 4to hard bound
ISBN 0 565 00818 £50.00

Amphipods are both numerous and diverse in numbers of genera and species in British coastal waters, but in the absence of any form of modern systematic synopsis or key this group of crustaceans has acquired the reputation of being notoriously difficult to identify. This monograph, which is the first comprehensive and illustrated text on British gammaridean amphipods to be published in more than a century, should go a long way towards solving the problem.

Titles to be published in Volume 37

Miscellanea

The echinoderms of Aldabra and their habitats. By N. A. Sloan, Ailsa M. Clark & J. D. Taylor

The Fellodistomidae (Digenea) of fishes from the northeast Atlantic. By Rodney A. Bray & David L. Gibson

The anatomy, phylogeny and classification of bariliine cyprinid fishes. By G. J. Howes

Printed by Henry Ling Ltd, Dorchester

Bulletin of the
British Museum (Natural History)

The echinoderms of Aldabra and their habitats

N. A. Sloan, Ailsa M. Clark &
J. D. Taylor

Zoology series Vol 37 No 2 20 December 1979

The *Bulletin of the British Museum* (*Natural History*), instituted in 1949, is issued in four scientific series, Botany, Entomology, Geology (incorporating Mineralogy) and Zoology, and an Historical series.

Papers in the *Bulletin* are primarily the results of research carried out on the unique and ever-growing collections of the Museum, both by the scientific staff of the Museum and by specialists from elsewhere who make use of the Museum's resources. Many of the papers are works of reference that will remain indispensable for years to come.

Parts are published at irregular intervals as they become ready, each is complete in itself, available separately, and individually priced. Volumes contain about 300 pages and are not necessarily completed within one calendar year. Subscriptions may be placed for one or more series. Subscriptions vary according to the contents of the Volume and are based on a forecast list of titles. As each Volume nears completion, subscribers are informed of the cost of the next Volume and invited to renew their subscriptions. Orders and enquiries should be sent to:

Publications Sales,
British Museum (Natural History),
Cromwell Road,
London SW7 5BD,
England.

World List abbreviation: *Bull. Br. Mus. nat. Hist.* (Zool.)

© Trustees of the British Museum (Natural History), 1979

ISSN 0007-1498

Zoology series
Vol 37 No 2 pp 81–128

British Museum (Natural History)
Cromwell Road
London SW7 5BD

Issued 20 December 1979

The echinoderms of Aldabra and their habitats

N. A. Sloan

Department of Zoology & Comparative Physiology, Queen Mary College, University of London,
Mile End Road, London E1 4NS. Interim address: Bermuda Biological Station for Research,
St George's West 1–15, Bermuda

Ailsa M. Clark & J. D. Taylor

Department of Zoology, British Museum (Natural History), Cromwell Road, London SW7 5BD

Contents

Synopsis 81
Introduction 81
Shallow water habitats of Aldabra 82
  Seaward habitats 83
  Lagoon and Channel habitats 83
Comparison between the echinoderm faunas of exposed and sheltered rocky shores 84
  Exposed rocky shore near Point Hodoul (407–080) 84
  Sheltered rocky shore on Ile Picard (056–100) 85
Ophiocomid microhabitats on Aldabra 89
  Associates of *Ophiocoma* species 93
Systematic account 93
  Class Crinoidea 95
    Subclass Asteroidea 95
    Subclass Ophiuroidea 99
  Class Echinoidea 117
  Class Holothurioidea 121
Acknowledgements 125
References 125

Synopsis

This first full account of the echinoderm fauna of Aldabra Atoll, western Indian Ocean, includes a description of the shallow-water habitats and two special ecological studies dealing with the microhabitats of the Ophiocomidae – the dominant family of coral-reef ophiuroids – and a comparison between the echinoderms of an exposed and a sheltered part of the shore. The remainder consists of an annotated fauna list, with details of habitats, colours in life, parasites, commensals and other observations on the individual species. It is based primarily on recent collections and observations by Sloan, but also takes account of previous work by others at the Royal Society's base on the atoll. Nearly 130 species are included, of which 20% are recorded for the first time from the islands of the western Indian Ocean (excluding the Mascarene Islands).

Introduction

Aldabra Atoll is a slightly elevated group of four main limestone islands which form a seaward rim with a maximum dimension of 34 km from east to west (see Fig. 1). It lies at 9°24′ S and 46°20′ E, some 650 km off the African mainland. With the exception of Assumption and Cosmoledo, Aldabra is isolated from all land by an oceanic basin. Its east and south seaward shores are the most exposed, being directly in the path of the SE trades, which blow constantly from April to November. During the other months more variable winds blow from the northwest. Detailed

Bull. Br. Mus. Nat. Hist. (Zool.) **37** (2) : 81–128 Issued 20 December 1979

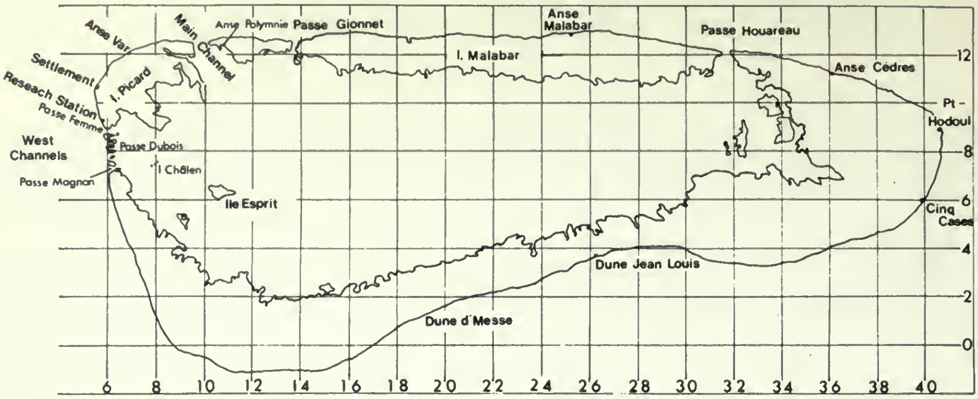


Fig. 1 Map of Aldabra showing localities mentioned in the text and the one kilometre square grid.

information on the climate, topography, tidal regime and many other aspects of Aldabra is available in Westoll & Stoddart (1971).

Collections of echinoderms from Aldabra were made during most phases of the Royal Society's Aldabra Expedition in 1967–1968, and between November 1977 and May 1978. Most of the collections have been deposited in the British Museum (Nat. Hist.). Thus there is sufficient material to warrant a report, as detailed reports on marine groups from this area are generally lacking. Zoogeographically Aldabra is somewhat isolated by being surrounded by the deep sea and comparisons between its echinoderm fauna and that of mainland Africa, the Mascarene Islands and Madagascar may be of interest.

This paper was initiated by one of us (N. A. S.) who made the observations, provided the photographs, the comparative study of two rocky shores and the section on ophiocomid microhabitats, as well as drawing up the systematic account after identification, or at least confirmation of identification, had been made by others. A. M. C. augmented the systematic account in some cases, confirmed or made all identifications except the majority of the holothurians, and supervised the literature references. J. D. T. provided the maps, some habitat information, and overall continuity of the habitat information. Dr F. W. E. Rowe identified most of the holothurians while on a study visit to London.

The ranges of 30 species are extended to the 'Islands of the western Indian Ocean' in the sense of Clark & Rowe (1971) (i.e. exclusive of the Mascarene Islands), plus a further nine species needing corroborative records. A new subspecies of *Ophiarachnella macracantha* is described and two subspecies of *Ophiolepis cincta* are recognized, prompting the revival of the long-synonymized name *O. garretti* Lyman, 1865.

The important study of Cherbonnier & Guille (1978) on the ophiuroids of Madagascar came to hand only after completion of the typescript of this paper but a few references to it have been inserted. It gives keys, descriptions, illustrations and habitat notes for a large proportion of the ophiuroid species now recorded from Aldabra.

Shallow water habitats of Aldabra

The general relationships of the major shallow water marine habitats are briefly described below and illustrated in Figs 1 & 2.

A nearly continuous land rim of Pleistocene limestones, breached in four places by narrow channels, surrounds a large shallow lagoon. On the seaward side of the Atoll the land is terminated by steep 4 m high cliffs, beyond which an intertidal or shallow sublittoral platform extends up to 450 m and ends abruptly at the steep seaward slope of the Atoll. The lagoon shoreline is extremely

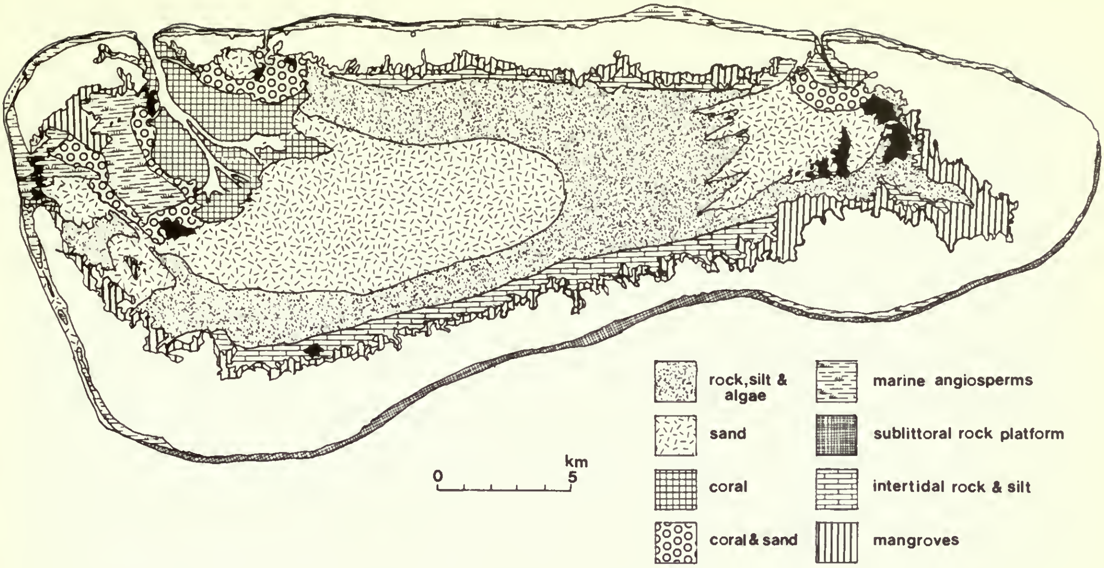


Fig. 2 Map of Aldabra showing the distribution of the major shallow water habitats.

irregular and almost completely fringed by mangroves growing upon rock or silty substrates. The rest of the lagoon is very shallow with a water depth rarely exceeding 5 m and with a rock bottom covered with a variable thickness of fine sands and silt. However, near the channels into the lagoon the hydrodynamics are much more complex and a mosaic of habitats is developed.

Seaward habitats

Most of the Atoll is fringed by intertidal cliffs which are ramp shaped on the exposed southerly and easterly shores but vertical or undercut at the more sheltered north and easterly sides. Subaerial, marine and biological erosion has produced severe dissection and topographic complexity on these cliffs and further details of the habitats may be found in Taylor (1971*a*) and Trudgill (1976). Along the only large intertidal beach on the Atoll, at the Settlement area on Ile Picard, there is an extensive development of beachrock over 1000 m long and 20–30 m wide. It occupies most of the upper eulittoral zone and the seaward dipping slabs of rock form a habitat for a diverse assemblage of echinoderms.

The base of the cliffs is continuous with the narrow seaward platform which virtually surrounds the Atoll; the platform is widest at the western and northern sides of the Atoll and narrowest in the east. At the western end where the platform is about 450 m wide it is mostly covered by a thin veneer of sediment and colonized by stands of marine grasses particularly *Thalassia* and *Thalassodendron*, but *Halodule* and *Cymodocea* also occur. The grasses grow upon medium grade sand, but cobbles and coral debris may be abundant. Small coral colonies may be common in the deeper parts of the platform, particularly *Millepora* and *Porites*. Large dune-like sand bodies migrate along the platform with the seasonal wind changes. Towards the seaward edge of the platform there is a belt about 30 m wide consisting of boulders and cobbles thrown up by wave action. The boulders rest upon calcareous algae covered rock or upon sand and rubble colonized by *Thalassodendron*. On the south and east shores the narrower platform is generally sediment free and colonized by an algal turf with *Laurencia*, *Dictyosphaera*, *Turbinaria*, *Cladophoropsis* and calcareous red algae.

Lagoon and Channel habitats

Except for the mangrove fringe, much of the central lagoon presents a generally monotonous, uniform habitat. The water is very turbid and the shallow more or less silt covered bottom is covered by sometimes extensive growths of algae; particularly common are *Halimeda*, *Cystoseira*, *Hydroclathrus*, *Sargassum* and *Caulerpa*, with abundant epilithic sponges.

However near the four lagoon channels, complex habitat mosaics are developed in response to the increased circulation produced by regular tidal flushing. Main Channel, the largest channel, has extensive and diverse coral growths along the edges of the channel and its complicated system of tributaries. More patchy habitats of sand and isolated coral colonies form an arc around the 'catchment' area and this habitat passes transitionally into that of the central lagoon, mentioned above. The smaller channel, Passe Houareau, has limited coral growth along its edges with more or less concentric arcs of marine grasses mixed sand and coral, and sandy habitats. Passe Gionnet, a small channel, has areas of coral, mixed coral and sand, and sand.

The greatest complexity of habitats is seen in the West Channels area where the land rim has been breached several times by narrow, shallow channels, only one of which, Passe Dubois, is deep enough to breach the seaward platform. Immediately within the lagoon behind the channels an extremely complex patchwork of habitats is developed in relation to the catchment of each of the minor channels. The main habitat types present include beds of marine angiosperms, particularly *Thalassia* and *Thalassodendron*, patches of abundant algae particularly *Gracilaria*, *Laurencia* and *Halimeda*, sand patches, mixed sand and coral habitats, and areas consisting of algally coated cobbles and boulders. Coral microatolls and growths of *Porites*, *Goniastrea*, *Pavona* and *Millepora* are common on the grass and sandy areas, whilst more extensive coral growth including *Millepora platyphylla*, branching *Porites* and *Goniastrea* occur within the channels.

Comparison between the echinoderm faunas of exposed and sheltered rocky shores

Exposed rocky shore near Point Hodoul (407–080)

This site was an extremely exposed shore in the form of an intertidal rock platform or bench which is described in more detail in Taylor (1971*a*). It projected about 65 m to the seaward from a small pocket sand beach and it was surrounded on the landward by an undercut limestone cliff. The rock platform was eroded quite smooth with numerous erosion pits, some of which contained sand retained by overlying trapped boulders. There were no boulders overlying the platform itself. This habitat sheltered an echinoderm fauna low in numbers but relatively high in species for this exposed shore. *Holothuria arenicola* was the most common holothurian and it occurred as infauna in the trapped sand, numbering up to three per pit. As cryptofauna under the boulders over the sand the following species: *Afrocucumis africana*, *Holothuria cinerascens*, *H. hilla*, *H. impatiens*, *H. leucospilota* and *H. pardalis*, *Echinoneus cyclostomus*, *Echinometra mathaei*, *Macrophiothrix longipeda* and *Ophiocoma scolopendrina* were fairly common, as was *Holothuria cinerascens* in larger crevices. The abundance of crevice-dwelling holothurians increased considerably while the numbers of *O. scolopendrina* diminished to seaward. Also in the lower eulittoral, small epibenthic *Actinopyga mauritiana* became more common in the rock pools. Some were only about 40 mm long, which is interesting as Bakus (1968) had difficulty in finding small specimens of this species on the Marshall Islands. Most noteworthy, however, were the great numbers of echinoids in burrows at the seaward end of the platform.

About 10 m landward from the low water spring level an escarpment about 60 cm high and 110 m long ran parallel with the water level. A strip along this escarpment 20 m wide on the landward and 10 m wide on the seaward side contained the area of highest echinoid and holothurian density. Fifty quadrats of 0·25 m^2 were sampled by random casting over the shoulder along this strip on each side of the escarpment and 25 vertically-orientated quadrats were sampled along the escarpment itself using random number tables. The results of the echinoid counts are listed in Table 1. The vertical escarpment face was dominated by the larger echinoid *Stomopneustes variolaris* while the horizontally-orientated burrows were usually filled with *Echinometra mathaei*. Table 2 shows the size differences of the burrows of these two species. Almost every burrow was occupied so the availability of burrows in this area could be a limiting factor affecting the population size of the echinoids. Their burrowing activities probably contribute to bioerosion on this

Table 1 Numbers of echinoids per 0·25 m² quadrat

	Echinoid counts	0	1	2	3	4	5	6	7	8	9	10	11	12	13	14	No. of quadrats sampled
Echinometra mathaei	above escarpment	30	12	2	6	–	–	–	–	–	–	–	–	–	–	–	50
Stomopneustes variolaris	above escarpment	46	3	–	–	1	–	–	–	–	–	–	–	–	–	–	50
E. mathaei	on escarpment	1	–	3	10	5	3	2	1	–	–	–	–	–	–	–	25
S. variolaris	on escarpment	–	–	1	4	3	3	–	5	1	3	3	1	–	–	1	25
E. mathaei	below escarpment	23	16	6	3	2	–	–	–	–	–	–	–	–	–	–	50
S. variolaris	below escarpment	45	2	2	1	–	–	–	–	–	–	–	–	–	–	–	50

Table 2 Sizes of echinoid burrows.

	No. of burrows	Mean depth (mm)	S.D.	Mean diameter (mm)	S.D.
Echinometra mathaei	40	67·4	5·1	39·7	3·4
Stomopneustes variolaris	40	117·0	8·5	85·5	7·0

shore (Taylor, 1971*a*; Trudgill, 1976). The echinoids remain permanently in their burrows which trap wave-transported drift algae and sea grasses.

There were two holothurian species, *Afrocucumis africana* and especially *Holothuria cinerascens*, which were common in this very pock-marked habitat. Up to 15 *H. cinerascens* were found tightly packed in a single vacant *S. variolaris* burrow and individuals were usually found wherever crevice or overhang spaces were available. *A. africana* was restricted to the smaller crevices although the two species were sometimes found together. Both these species are passive suspension feeders that trap suspended food on their sticky tentacles. The holothurians and the echinoids did not, however, coexist in the same burrows. The *E. mathaei* from the exposed south coast were larger than anywhere else on the atoll. Similarly, Khamala (1971) in Kenya and Russo (1977) in Hawaii both reported that *Echinometra mathaei* from areas of the strongest wave action were the largest. Interestingly, there were no *Echinostrephus molaris* in the lower eulittoral here although they were present on more sheltered seaward shores of the west and north coasts.

In summary, this exposed shore was dominated by echinoids in the lower eulittoral although two species of holothurians were quite common. A small population of six holothurians, two echinoids and only two ophiuroids occurred in the mid and upper eulittoral. The conspicuous dearth of ophiuroids in this habitat is noteworthy and is probably due to the exposed nature of this rocky shore.

Sheltered rocky shore on Ile Picard (056–100)

This shore consisted of a series of eroding slabs of beach-rock in the upper eulittoral with a sandy beach to the landward side and a grass pool to seaward. This area is described in detail in Taylor (1971, 1976) and Sloan (in press). There were boulders overlying intact bedrock here, unlike the exposed shore, probably because of the less violent wave action. These boulders provided shelter for cryptofauna and numerous holothurians occurred under them. The most common species were the suspension feeder *Afrocucumis africana* and the four deposit feeders, *Polycheira rufescens*, *Holothuria parva*, *H. impatiens* and *H. leucospilota*. The first three of these species were quite common and detailed information on the distribution and abundance of this fauna is provided in Sloan (in press). Other uncommon holothurians from the beach-rock were *H. cinerascens*, *H. atra*, *H. rigida*, *H. arenicola* and *H. moebii*. Echinoids were rare in this area and a total

Table 3 Published data on ophiocomid microhabitats, including those of three species from the tropical West Atlantic

Species	Author(s)	Notes
Ophiocoma brevipes	H. L. Clark (1921)	Mer, Murray Islands, Torres Strait: on sand under coral
	H. L. Clark (1946)	Murray Islands and Lord Howe Island; noted a crevice-dwelling habit and a tendency of individuals to fold their arms closely around the disc
	Devaney (1967)	Hawaii; under boulders overlying sand in which they were partially buried. Not found on coarse gravel or cobble
	Taylor (1968) Taylor & Lewis (1970)	Mahé, Seychelles: 'abundant' on grass beds under coral boulders and in the bases of living coral
	Taylor (1971*b*)	Diego Garcia, Chagos Islands: crevice dwelling on seaward platforms, in *Thalassodendron* beds, 'abundant' on lagoon platforms covered by *Thalassodendron* and coral heads
	Chartock (1972)	Eniwetok Atoll, Marshall Islands: in the lower eulittoral under coral in small crevices and 'firmly set' boulders of the algal ridge, up to 2 per m² in 'optimum' habitat
	Devaney (1974)	Southeastern Polynesia: 'a rather specific habitat' under coral heads and boulders over sand on reef flats, usually 1 or 2 per boulder, most numerous under coral heads; may partially bury themselves in the sand
Ophiocoma doederleini	Chartock (1972)	Eniwetok Atoll: most common species of the *brevipes* subgroup (*O. brevipes*, *O. dentata*, *O. doederleini*), under 'firmly placed' boulders and coral heads overlying gravel and detritus, rarely more than 1 per boulder and up to 1 per m²
	Devaney (1974)	SE Polynesia: on 'relatively clean' sand under boulders at a depth of 1–10 m. Note: Both Chartock (1972) and Devaney (1974) mention the similarity between the microhabitats of *O. doederleini* and *O. dentata*
Ophiocoma erinaceus	H. L. Clark (1921)	Torres Strait: 'very common' in heads of *Pocillopora*, *Acropora* and *Seriatopora* but not common on the sand under these heads, a 'more active species than *O. scolopendrina*' in its behaviour when disturbed. Stressed the 'complete separation of habitat' between *O. erinaceus* and *O. scolopendrina*
	H. L. Clark (1946)	Torres Strait, Murray Islands and Lord Howe Island: mentioned this species as being 'so frequently confused' with *O. scolopendrina*, often found in 'dead and dying' coral heads
	Balinsky (1957)	Inhaca Island, off Mozambique: considered a 'rare' species in coral in some shores, but common on 'more tropical' reefs in that area
	Taylor (1968) Taylor & Lewis (1970)	Mahé: 'less common' than *O. scolopendrina* and *O. brevipes* on grass beds and 'more abundant' in reef edges, fronts and algal ridges
	Taylor (1971*b*)	Diego Garcia: common cryptofauna on seaward platform and the algal ridge
	Fishelson (1971)	Gulf of Aqaba: probably some confusion here between *O. erinaceus* and *O. scolopendrina*; (p. 126) crevice fauna in extended intertidal beach-rock plates densities of 150–200 per m² were recorded, on limited beach-rock the population is compressed into a band 'along the *Tetracleta* colonies'. (p. 131) names this species as using the feeding methods well described for *O. scolopendrina*

	Chartock (1972)	Eniwetok Atoll: the most abundant and widespread *Ophiocoma* species, maximum densities in heads of *Heliopora coerulea* of 6 per 0·002 m^3 (or 6×10^3 per m^3), also found in *Pocillopora* heads and occasionally in *Acropora* and *Millepora*, most numerous in proximal region of the coral heads. Heads of 0·01 m^3 frequently had 15 *O. erinaceus* present in crevice habitats, up to 5 per m^2
	Devaney (1974)	SE Polynesia: in live and dead coral heads like *Acropora* and *Pocillopora* and under boulders, less common on sandy and more common on more solid substrates
	Hughes (1977)	Jeddah, Saudi Arabia: 'replaces' *O. scolopendrina* to the seaward on reef flats
Ophiocoma pica	H. L. Clark (1921)	Torres Strait and Lord Howe Island: not common; coral head infauna like *O. erinaceus*
	H. L. Clark (1946)	Torres Strait: not common, 'very secretive habitats' in coral heads
	Balinsky (1957)	Inhaca Island: seen only on 'more tropical' reef at Ponta Torres
	Devaney (1970)	Hawaiian Islands and others in that area: most common in heads of *Pocillopora meandrina* var. *nobilis*, smaller specimens very common in coral whereas larger individuals can be found under boulders, coral rubble and living coral
	Chartock (1972)	Eniwetok Atoll: common in living and dead *Heliopora coerulea*, but preferred *Pocillopora elegans*, and occasionally under rocks and in crevices. Less common than *O. erinaceus* in coral heads, and tended to occupy the distal areas of coral heads in contrast to *O. erinaceus*
	Devaney (1974)	SE Polynesia: confirmed strong association with *P. meandrina* and suggested that young may settle in these heads preferentially, adults may be found under coral and in 'non coral' habitats
Ophiocoma pusilla	Balinsky (1957)	Inhaca Island; a 'rare' member of the coral infauna but more common on the 'more tropical' reefs and in dead coral heads
	Devaney (1970)	Eniwetok and SE Polynesia; in shallow sublittoral areas occurs as coral infauna, in both live and dead coral and under coral rubble, 'confined to the shallow sublittoral zone within a coral substratum'
	Devaney (1974)	SE Polynesia: a specimen from Hawaii on black coral *Antipathes* from 70 m, generally found in shallow areas in or under live or dead coral
Ophiocoma scolopendrina	H. L. Clark (1921)	Torres Strait: very common 'occupies a restricted and peculiar habitat near high-water mark' as crevice fauna, first descriptions of the characteristic 'swaying arms' of this species at the air–water interface during a flood tide and suggested at least a respiratory function if not a feeding function for this
	Balinsky (1957)	Inhaca Island: 'abounds' under algal mat at the fringe of *Cymodocea* (*Thalassodendron*) beds on sand flats
	Magnus (1967)	Egyptian and other tidal Red Sea coasts: as crevice fauna on sheltered rocky shores between middle and low tides, up to 50 per m^2. The first worker to describe in detail the unique feeding methods of this species at the air–water interface during flood tides
	Devaney (1970)	General distribution: confirms 'restricted littoral habitat' of this species
	Taylor & Lewis (1970)	Mahé: 'abundant' under coral boulders and in the bases of living corals, possible confusion here with *O. erinaceus*

Species	Author(s)	Notes
	Fishelson (1971)	Gulf of Aqaba: see above for *O. erinaceus*, there could be some confusion between these two species here
	Taylor (1971*b*)	Diego Garcia Atoll: on seaward platform, 'abundant' in crevices of the algal ridge, abundant on lagoon platforms covered with *Thalassodendron* and coral heads, could be confused with *O. erinaceus* here
	Chartock (1972)	Eniwetok Atoll: 'upper intertidal zone' as crevice fauna on rocky shores sheltered from 'intense surf', up to 100 per m^2 but 20 per m^2 more common
	Devaney (1974)	SE Polynesia: in coral rubble and coarse sand in the intertidal zone on reef flats and barrier reef platforms, densities of up to 50 per m^2
	Hughes (1977)	Jeddah: 'abundant under loose stones on the higher intertidal of reef flats'
Ophiocoma valenciae	Balinsky (1957)	Inhaca Island; not common in algal mat of the fringe of *Cymodocea* (*Thalassodendron*) beds, found once among coral, rare as cryptofauna under rocks of lower eulittoral but common in a 'more tropical' reef area
	Taylor (1968)	Mahé: common on grass beds and 'sand and cobble ridges' seaward of grass beds
Ophiarthrum elegans	H. L. Clark (1921)	Green Island, Queensland: 'very common . . . under rocks and coral fragments on the reef flats'
	Devaney (1974)	SE Polynesia: in live coral and under coral and rubble, 'common under coral colonies on white sand' along with *O. dentata* and *O. doederleini*
Ophiomastix caryophyllata	H. L. Clark (1921)	Torres Strait: 'quite common in dead portions of coral colonies on the . . . reef flat'
Ophiocoma echinata	Kissling & Taylor (1977)	Florida keys: turbulent reef flats, areas with ample rubble cryptohabitat and a coarse substrate
Ophiocoma pumila	Kissling & Taylor (1977)	Florida keys: as for *O. echinata* above
Ophiocoma wendti	Kissling & Taylor (1977)	Florida keys: as for *O. echinata* and *pumila* but less common and not so strongly correlated with turbulent areas [Abundance of the last three species increases with the amount of local 'sub-rubble' shelter]

of eight individuals of the following species were found; *Echinoneus cyclostomus, Eucidaris metularia, Tripneustes gratilla* and *Echinothrix calamaris. Ophiocoma scolopendrina*, the only ophiuroid in this area, occurred in great numbers, especially under boulders over rubble at the seaward end of the beach-rock, see site 1 in Table 4.

The difference in the echinoderm fauna between the exposed and sheltered beach-rock sites is noteworthy although the latter site occupied only the upper eulittoral which the former occupied both the upper and lower eulittoral. Firstly, there was the predominance of deposit-feeding holothurians over suspension-feeding ones on the sheltered shore. Although *Afrocucumis africana* was the most common species on the sheltered shore in terms of numbers, this small species was greatly overshadowed in relation to total holothurian biomass and *H. cincerascens* was rare (only three found). Secondly, echinoids were much less common on the sheltered shore, although they are not generally well adapted to life in the upper eulittoral. (For instance, *Stomopneustes variolaris* was not present on the sheltered shore.) There was no comparable dominance by echinoids in the lower eulittoral of the whole seaward platform of the sheltered shore of the west coast although echinoids, at least six species, were more common under the boulders of the lower eulittoral overlying sandy gravel than in the upper eulittoral overlying the bedrock. Finally, ophiuroids were much more abundant on the sheltered rocky shore. Also their species diversity, at least ten species, increased in the lower, non-rocky, eulittoral of the sheltered shore platform. Ophiuroids, being less robust in construction compared to echinoids and holothurians, find exposed wave-washed shores less amenable habitats.

The few species able to exploit successfully the rigorous conditions of the exposed shore clearly find it a productive environment. The two echinoids make their own cryptohabitat by burrowing while the two holothurians exploit crevice space and vacant burrows. There are no appreciable quantities of deposited food but plenty of suspended material is made available by wave action. The relative lack of cryptohabitat on the vigorously scoured exposed shore compared to the boulder-strewn sheltered shore is an important factor in the establishment of a deposit-feeding holothurian cryptofauna on the sheltered shore.

Ophiocomid microhabitats on Aldabra

The most prominent family of shallow-water tropical ophiuroids is the Ophiocomidae and one of its genera, *Ophiocoma* Agassiz, 1836, dominates among coral reef ophiuroids (A. M. Clark, 1976*b*). All ophiocomids are cryptic and live in crevices, in or under boulders and coral heads, and at the bases of sea grasses and algae. They can be present in great numbers and dominate the local echinoderm cryptofauna and indeed all the cryptofauna. With the exception of Chartock's (1972) study of 'niche separation' among seven *Ophiocoma* species from Eniwetak Atoll, Marshall Islands, observations on the ecology of this important group are scattered and generally anecdotal. Some interesting recent observations on ophiocomid microhabitats from the literature, starting with H. L. Clark's (1921) Torres Strait paper, are listed in Table 3. These will be compared with recent findings on the Aldabran ophiocomid species.

Table 4 lists a quantitative assessment of the microhabitats of Aldabran ophiocomids from the eulittoral and shallow sublittoral. Deeper areas were not sampled extensively as they were much less productive. The microhabitats sampled were:

1. (056–100) An upper eulittoral site where the slabs of beach-rock overlying rubble had been eroded from a band of intact beach-rock to the landward. These loose slabs remained immersed throughout neap tides since a seaward pool, formed by a further seaward sand bar, could not completely drain during these tides. The sand bar, however, was quite mobile, so the size and depth of this pool, and therefore the immersion time of slab-over-rubble microhabitat, was quite variable. The slabs were measured, drawn to scale on graph paper, the cut-out weighed, and thus their area calculated. The ophiuroids under these slabs were identified and counted. They were also weighed moist but free of excess water and debris.

2. (054–091) A lower eulittoral site consisting of a dense stand of *Thalassodendron ciliatum* (For-

Table 4 Microhabitats and weights of species of ophiocomids on Aldabra

Habitat	Number of Boulders(*) Coral heads($^{\Delta}$)	Total area m²(†) m³(‡)	Mean number of ophiuroids per boulder(*), m²(†), coral head ($^{\Delta}$)											
			Ophiocoma brevipes	*O. doederleini*	*O. erinaceus*	*O. pica*	*O. pusilla*	*O. scolopendrina*	*O. valenciae*	*Ophiomastix caryo-phyllata*	*O. koehleri*	*O. venosa*	*Ophiarthrum elegans*	Totals
1	32*	6·1†	0	0	0	0	0	10·25* 53·50†	0	0	0	0	0	10·25* 53·50†
2	62*	–	0·76*	1·38*	0·56*	0·02*	0·68*	0	0	0	0	0	0	3·40*
3	100*	–	2·74*	0·24*	0·04*	0	0·46*	0	0·02*	0	0	0	0	3·50*
4	100*	–	0·08*	0·04*	1·84*	0·06*	0·68*	0	0	0	0	0	0	2·70*
5	–	10·00†	0	0	0	0	0	0·41†	121·80†	0	0	0	0	122·21†
6	45$^{\Delta}$	19·29†	0·22$^{\Delta}$	2·87$^{\Delta}$	4·91$^{\Delta}$	1·00$^{\Delta}$	3·07$^{\Delta}$	0	0·04$^{\Delta}$	6·80$^{\Delta}$	0·02$^{\Delta}$	0·22$^{\Delta}$	0·76$^{\Delta}$	19·91$^{\Delta}$ 46·3†
7	40$^{\Delta}$	1·60‡	0	0·08$^{\Delta}$	7·03$^{\Delta}$	0·40$^{\Delta}$	0·70$^{\Delta}$	0	0·18$^{\Delta}$	1·62$^{\Delta}$	0	0	0	10·28$^{\Delta}$
8	40$^{\Delta}$	0·60‡	0	0	1·63$^{\Delta}$	0	0·15$^{\Delta}$	0	0	0·13$^{\Delta}$	0	0	0	1·91$^{\Delta}$

	Ophiocoma brevipes	*O. doederleini*	*O. erinaceus*	*O. pica*	*O. pusilla*	*O. scolopendrina*	*O. valenciae*	*Ophiomastix caryo-phyllata*	*O. koehleri*	*O. venosa*	*Ophiarthrum elegans*
Sample size	208	227	1200	108	360	975	1218	376	1	10	34
Mean wt(g)	1·42	2·78	4·33	2·45	0·18	4·55	2·53	2·18	4·02	10·78	4·98

skaal) on a wave-washed platform with occasional erosional pits filled with boulders. Ophiuroids were common on the platform only under the occasional boulder and rubble patches that overlay sandy gravel and some small rubble. The sea-grass root mat was very strong indeed and thus maintained the integrity of this habit. To landward the platform consisted of mixed stands of *Thalassia* on sandy, higher profile areas and *Thalassodendron* on rubble and in depressions with standing water – as far as the sandy beach.

3. (054–091) A very sandy site adjacent at the lower eulittoral to site (2). This is an area of numerous boulders where the sea-grass, probably *Thalassodendron*, although reduced to a worn stubble, still provided the substrate with some degree of stability. Under the boulders was fairly fine white sand. The reduced state of the sea-grass could be due to gradual inundation by sand as, to the landward, there was a large sand bar bordering sand flats with little sea-grass to prevent erosion of the substrate during rough weather. Ophiuroids were present only as cryptofauna.

4. (054–091) An area on the other side of site (2) of firmly placed boulders over coarse rubble with some trapped sand. The boulders were 'cemented' together with deposited gravel in irregular groups that contributed a marked third dimension to this habitat, unlike sites (2) and (3) above. To landward a *Thalassodendron* platform was present, being elevated on an approximately 25 cm escarpment. Ophiuroids were present only as cryptofauna.

5. (065–090) This lagoon habitat, a short distance from the northernmost western channel, was a sand flat covered with a dense stand of *Thalassia hemprichii* (Ehrenb.) with abundant algal *Halimeda* sp. and *Gracilaria* sp. (see Hughes & Gamble, 1977, p. 336). The *Thalassia* formed a substrate for a considerable epiphytic algal mat. This area drained for up to 3 h after low tide but never completely dried out as there was always a residual 2–3 cm of standing water present. Interestingly, on slightly higher sandy substrates in this area that drained fully at low tide, there was sea-grass but much less algae present and a greatly reduced epifauna. Ophiuroids were present as cryptofauna at the bases of the sea-grass and under or in the algae.

The next three microhabitats come from the same area. This was another lagoon habitat (068–083) adjacent to Passe Dubois of the West Channels. It consisted of discrete patches of coral heads in a matrix of dense sea-grasses, mostly *Thalassodendron* and some *Thalassia*. This was a sublittoral habitat as a residual 10–15 cm of water was present at the lowest ebb of the tide. The ophiuroids here were either in or under the three types of coral head microhabitat.

6. Microatolls of *Porites lobata* Dana up to 1·20 m in diameter. It should be noted, however, that other potentially microatoll forming *Porites* species occur on Aldabra (Rosen, pers. comm.). They are *P.* sp. cf. *P. luta* Edwards and Solander, *P. australiensis* Vaughn, and *P. somaliensis* Gravier. The microatolls formed a cryptic microhabitat covering sandy gravel.

7. Coral heads of *Porites nigrescens* Dana of up to 55 kg. Ophiuroids occurred here mainly as infauna.

8. Coral heads of *Millepora exacea* Forskaal of up to 7·60 kg. Ophiuroids occurred almost completely as infauna. The relatively small heads of this hydrocoral had much smaller interstitial spaces than *P. nigrescens* above. Although relatively barren of ophiocomids, this was a production microhabitat for ophiotrichids such as *Ophiothrix* (*Keystonea*) *propinqua*.

General distribution notes on these ophiocomid species around the whole of Aldabra are given in the systematic account. All the species were most common on the more sheltered shores like the seaward platforms of the coast and lagoon flats, so their microhabitats were examined in these areas. The only ophiocomid excluded here is the diminutive *Ophiocomella sexradia*, since estimates of its abundance are unreliable due to sampling error.

Ophiocoma brevipes: This relatively small species was most common at site 3 where it occurred partly buried in sand under boulders in the lower eulittoral. Up to 14 specimens were found under one boulder, compared with a population of only two per m^2 in Chartock's (1972) optimum habitat. This is the most sand-loving *Ophiocoma* species on Aldabra, as well as in other parts of its range, as listed in Table 3. Interestingly, *O. brevipes* was uncommon both under microatolls over sandy substrates in the shallow sublittoral of the lagoon (site 6) and also relatively rare throughout the sublittoral, regardless of substrate.

Ophiocoma scolopendrina: This species is widely reported as common in the upper eulittoral of rocky shores throughout its range. Aldabra is no exception, the species occurring in crevices or under boulders in large numbers in the Ile Picard beach-rock at site 1. This was the only ophiuroid present in an upper eulittoral habitat and was only rarely found in the lower eulittoral or the sublittoral.

Ophiocoma valenciae: Like *O. scolopendrina*, this species was very particular, abundant in its chosen habitat and rare elsewhere. *O. valenciae* dominated at site 5 on the sheltered grass flats in the bases of sea-grass covered with algal mat and standing water throughout low tide. It was rarely found elsewhere in the eulittoral or the sublittoral. In 1968 Taylor reported that this species was common in areas seaward of grass beds as well as in the grass beds themselves.

Ophiocoma doederleini: In the lower eulittoral this species was abundant on coarser substrates such as gravel or rubble under boulders but even more numerous, however, in the shallow sublittoral under the microatolls at site 6. There are few positive records from the literature because of confusion with *O. dentata* (formerly *insularia*) but the two references do list a similar microhabitat of sandy gravel under boulders in shallow water. Unlike the findings of Chartock (1972) on Eniwetok, on Aldabra this species is much less solitary, up to 16 specimens being found under a single microatoll.

Ophiocoma erinaceus: A large species and the most ubiquitous ophiocomid in the lower eulittoral and shallow sublittoral. In the lower eulittoral it dominated under boulders in the most rocky habitat, site 4. It was common under the microatolls and abundant as coral head infauna in site 7 (*P. nigrescens*) and indeed in all corals with large interstitial spaces. This species is well known in the literature as coral head infauna and cryptofauna under boulders, although less mention is made of its marked preference for rocky rather than sandy substrates. Also, there has been some confusion between it in the past and the upper eulittoral rocky shore species *O. scolopendrina*.

Ophiocoma pica: Not a common species on Aldabra where it was generally restricted to the shallow sublittoral in association with coral. Fairly common in heads of *P. nigrescens* but abundant under the microatolls in site 6; reported in the literature as coral head infauna rather than cryptofauna. Devaney (1970) noted that larger specimens could be found as cryptofauna and this is also true on Aldabra.

Ophiocoma pusilla: This little species is suspected to be more common than appears from Table 2. Being small and highly active when disturbed makes thorough collecting difficult. On Aldabra *O. pusilla* is rather an ubiquitous species in the lower eulittoral, although less common on the sandy substrates. Therefore it was not confined to the shallow sublittoral, as Devaney (1970) reported it to be at Eniwetok and S.E. Polynesia. In the sublittoral of Aldabra it was abundant under the microatolls, although present also as coral head infauna.

Ophiomastix caryophyllata: The dominant ophiocomid under the microatolls at site 6 and common also as coral head infauna. This rather fragile species is interesting as it could be an important competitor with *Ophiocoma* species in coral microhabitats in the shallow sublittoral of Aldabra. Restricted to the sublittoral and reported elsewhere as a dead coral infauna species.

Ophiomastix koehleri: The only specimen was found under a microatoll. Probably a sublittoral species but this requires confirmation from other areas.

Ophiomastix venosa: The largest ophiocomid on Aldabra. Basically restricted to the sublittoral although occasionally found under rubble in standing water, like *Ophiarthrum elegans* below, in the eulittoral of seaward platforms. It was collected particularly under microatolls at site 6 although it could not be considered a common species. No references were found to the habitats of this species.

Ophiarthrum elegans: A fairly common species whose sublittoral microhabitat compares with the two references in Table 3. It was most common at site 6 under the microatolls but uncommon as coral head infauna.

The greatest diversity of ophiocomids and indeed ophiuroids as a whole was under the sublittoral microatolls in the lagoon at site 6. The area is one of persistent tidal currents providing quantities of suspended food yet it is sheltered from disruptive wave action. The patches of coral heads were surrounded by grass beds in which the ophiuroids could perhaps forage at night while protected from predatory fish like wrasses.

The success of *Ophiocoma* species throughout the tropics could be related to their robust form and adaptability. They can occupy less benign eulittoral microhabitats as well as the sublittoral ones from which other related genera are excluded. Indeed, no other ophiuroid genus, of any family, is so well represented on tropical eulittoral shores. Having the resilience to cope with the rigours of eulittoral existence may have enhanced the competitive ability of *Ophiocoma* species in the shallow sublittoral, although *Ophiomastix*, as a successful specialist in this area, must be contended with. The monopolization by *O. scolopendrina* and *O. valenciae* of their particularly rigorous microhabitats is clearly a highly successful strategy. Temperature tolerance, up to 40 °C for *O. scolopendrina* (Chartock, 1972), at low tide at midday would be an essential prerequisite for life in both these microhabitats. A tolerance to lowered salinity due to periodic tropical downpours would also be important. Both species belong to different morphological subgroups of *Ophiocoma* (Devaney, 1970) so that the evolutionary potential to withstand physiological stress is perhaps a characteristic of the genus as a whole. Interestingly, *O. anaglyptica* Ely, a member of the *scolopendrina* subgroup, dominates under dead coral and rubble in the algal ridge (sublittoral fringe) of seaward platforms at Eniwetok Atoll to the virtual exclusion of other ophiuroids (Chartock, 1972). It was present in its preferred area at densities of up to 150 per m^2 (240 g per m^2).

Kohn (1971) suggested that co-occurring non-predatory tropical marine invertebrates are more likely to have a specialized microhabitat than specialized food type, as do predatory gastropods. Chartock (1972) supported this hypothesis through his observations on the seven *Ophiocoma* species at Eniwetok Atoll. He found that the ophiuroids were 'apparently non-selective' general detritus feeders with significantly different microhabitat specializations. In this present study, each of the *Ophiocoma* species demonstrated appreciable differences in their microhabitat or combination of microhabitat choices. It seems likely that on Aldabra, like Eniwetok, the availability of and competition for suitable cryptic microhabitats influences the presence of ophiocomids.

Associates of *Ophiocoma* species

A wide range of macroscopic animals occur in association with species of ophiocomids, some recorded from the present collection and others from the literature. References to those found with Indo-West Pacific species of *Ophiocoma* are given in Table 5.

Systematic account

It should be mentioned that only three ophiuroid species out of the 41 listed in Hughes & Gamble (1977) can be confirmed by us. Their specimens were incinerated to obtain the ash-free dry masses to estimate biomass per metre^2 for each species. They do, however, cite Dr F. W. E. Rowe as having checked their holothurian identifications.

Dr R. N. Hughes has kindly supplied us with an unpublished appendix upon which the paper of Hughes & Gamble is based, while Dr W. F. Humphreys has also made available to us his Aldabra specimens and an unpublished list of preliminary identifications of them made in 1971. His contribution has added ten confirmed species new to the fauna of Aldabra.

Throughout this account, references are kept to a minimum by citing major works when possible, such as Clark & Rowe (1971) or Rowe & Doty (1977), from which the original species descriptions can be traced. After these citations there are in some cases biological references to the species. These are included as an indication of the available biological information.

Table 5 Associates of Indo-west Pacific *Ophiocoma* species

Host species	Associate species		Locality	Authority
Ophiocoma anaglyptica	*Hololepidella nigropunctata* (Horst)*	– polychaete	Eniwetok, Marshall Is.	Devaney (1967)
O. brevipes	*H. nigropunctata*		Hawaiian Is.	Devaney (1967)
	H. minuta (Potts) (*H.* = *nigropunctata*)*		Solomon Is.	Gibbs (1969, 1971)
	H. nigropunctata		Aldabra	This paper
	Gyptis sp.	– polychaete	Aldabra	This paper
O. dentata (as *O. insularia* Lyman)	*H. nigropunctata*		Hawaiian Is.	Devaney (1967)
	H. minuta (= *H. nigropunctata*)		Solomon Is.	Gibbs (1969, 1971)
	H. nigropunctata		Northern Great Barrier Reef	Gibbs *et al.* (1976)
	Halicarcinus orientalis Sakai	– crab	Japan	Takeda *et al.* (1976)
O. doederleini	*Hololepidella nigropunctata*		Marquesa Is., Polynesia	Devaney (1974)
	H. nigropunctata		Aldabra	This paper
	Anoplodactylus ophiurophilus Stock	– pycnogonid	Aldabra	Sloan (1979)
O. erinaceus	*H. nigropunctata*		Hawaiian Is.	Devaney (1967)
	A. ophiurophilus		Aldabra	Sloan (1979)
O. pica	*A. ophiurophilus*		Aldabra	Sloan (1979)
O. scolopendrina	*Gyptis ophiocomae* Storck & Niggeman		Red Sea	James & Pearse (1969)

* Gibbs (1969) proposed synonymizing *Hololepidella nigropunctata* (Horst) [in Devaney (1967)] with *H. minuta* Potts but later, Gibbs (1971) suggested that the name *H. minuta* should be discarded owing to taxonomic problems and the use of *H. nigropunctata* is preferable.

Class **CRINOIDEA**

COMASTERIDAE

Comanthus sp. juv.
One specimen taken from within the coral frame-work on a patch reef in the Main Channel lagoon drainage system (104–110).

MARIAMETRIDAE

Lamprometra klunzingeri (Hartlaub, 1890)
See: A. H. Clark, 1941 : 527; A. M. Clark, 1972 : 102.
One specimen; taken during daytime from under a coral overhang 25–30 m deep off the research station beach (053–091).

Range extended from East Africa and Madagascar.

Stephanometra indica (Smith, 1876)
See: A. H. Clark, 1941 : 436; A. M. Clark, 1972 : 107.
During daytime specimens were collected from under overhangs of patch reefs in the Main Channel drainage system (104–110), under coral heads on the lagoon grass flats near the West Channels (068–083), in Passe Dubois (060–080), 25–30 m deep off the research station (053–091), and commonly on rubble at the entrance of Passe Houareau (316–122).

COLOBOMETRIDAE

Oligometra serripinna (Carpenter, 1881)
See: A. H. Clark, 1947 : 216; A. M. Clark, 1972 : 129.
One specimen taken from under rubble in Passe du Bois (060–080).

ANTEDONIDAE

Dorometra mauritiana (A. H. Clark, 1911)
See: A. H. & A. M. Clark, 1967 : 69; A. M. Clark, 1972 : 141.
Abundant in the coral frame-work on patch reefs, especially *Acropora* patches in the Main Channel drainage system (104–110) and (120–080) during the daytime.

Colour in life: uniform pale green, mauve, orange or purple.

Range extended from the Mascarene Islands.

Subclass **ASTEROIDEA**

ASTROPECTINIDAE

Astropecten polyacanthus phragmorus Fisher, 1913
See: A. M. Clark, 1974 : 433.
Only reported by Hughes & Gamble (1977) (as *A. phragmorus*) and listed as coming from the east side of Passe Houareau (318–118). We think that this specimen was more likely to be *A. polyacanthus*, recorded below.

Astropecten polyacanthus Müller & Troschel, 1842
See: Fisher, 1919 : 63; A. M. Clark & Rowe, 1971 : 44.
One found washed up on West Point (056–106) (R = 59 mm) and another from sand patch in the West Channels (060–070 to 060–090) (R = 56 mm).

GONIASTERIDAE

Stellaster sp. juv.
One specimen from algae (*Gracilaria* & *Laurencia*) on *Thalassia* in the West Channels (060–070 to 060–090).

OREASTERIDAE

Culcita schmideliana (Retzius, 1805)
See: Jangoux, 1973*a* : 18; Thomassin, 1976 : 51 (feeding and ecology).

Juvenile (R = 12–15 mm) and subadult (R = 33 & 34·5 mm) found in the lower eulittoral under coral rubble on the seaward platforms of the west (054–091) and north (140–125) (241–127) coasts. Adult forms (R = 44 & 48 mm) found under rubble in standing water in the depression of the Anse Malabar cliff base (241–127).

Colour in life of juveniles: medium green with occasional orange blotches, subadults pale orange and adults pale green with rich blue spines.

Protoreaster lincki (de Blainville, 1834)
See: Jangoux, 1973*a* : 23; Thomassin, 1976 : 51 (feeding & ecology).
Interestingly, all were juveniles (mean R = 28·2 mm for the eight specimens) washed up on the sandy beach in front of the research station (054–091). The animals must have come from the seaward grass flats although intensive searching among the grass beds failed to yield specimens.

Colour in life: cryptic mottled blue-green, in contrast to the adult colour of red on pink or pinkish-grey ground.

OPHIDIASTERIDAE

Dactylosaster cylindricus (Lamarck, 1816) Fig. 4
See: H. L. Clark, 1921 : 85.
Two specimens (R = 54 & 57·5 mm) found under boulders over coarse rubble in the lower eulittoral off the research station (054–091).

Colour in life: the shiny skin uniform burgundy.

Fromia milleporella (Lamarck, 1816)
See: H. L. Clark, 1921 : 40; Marsh, 1977 : 257.
One specimen (R = 25 mm) found on coral at 15 m depth off the research station (052–091).

Colour in life: deep purple above, much paler below.

Range extended from the Mascarene Islands, East Africa and Madagascar.

Leiaster sp. juv.
One specimen from algal mat on *Thalassia* in West Channels (060–070 to 060–090).

Linckia guildingi Gray, 1840
See: H. L. Clark, 1921 : 67.
Six specimens (mean R = 33 mm) taken from *Porites* and *Goniastrea* microatolls in Passe Houareau (316–120).

BMNH records (unpublished, see A. M. Clark & Rowe, 1971 : 36) include specimens from Curieuse, Platte and Moyenne Is of the Seychelles.

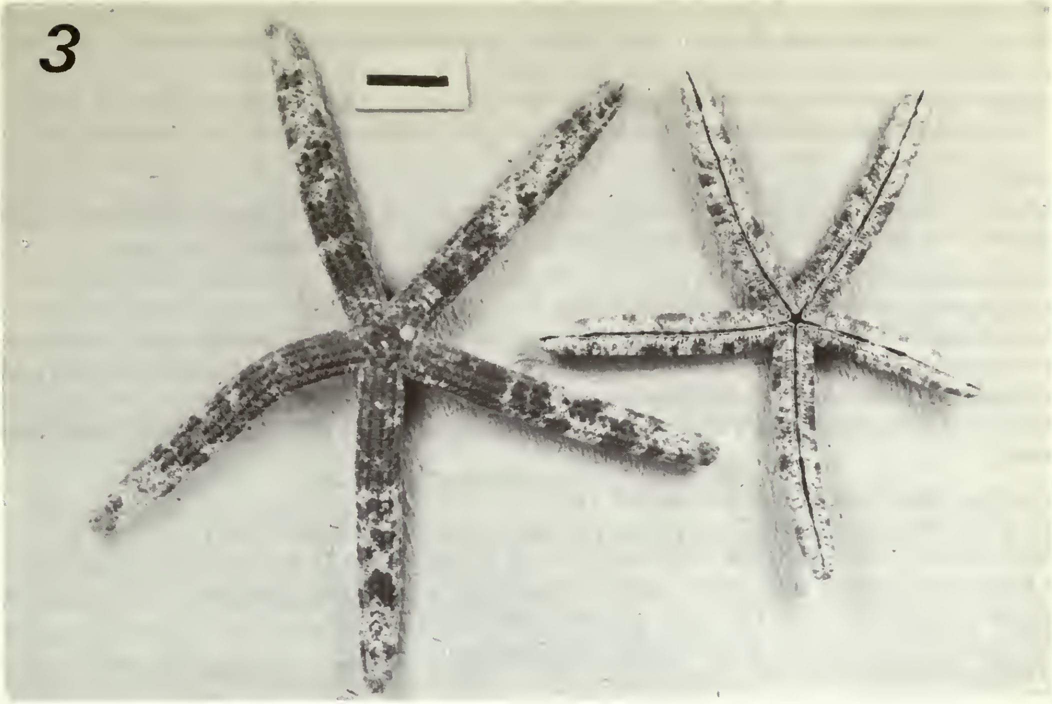
Linckia laevigata (Linnaeus, 1758)
See: Jangoux, 1973*a* : 29; Laxton, 1974 : 47 (feeding & ecology); Yamaguchi, 1977*a* : 13 (growth, reproduction, population structure).
Two specimens (R = 161, 169 mm) taken from coral flats in the Main Channel drainage system in the lagoon (108–120) where it was fairly common.

Colour in life: uniform light blue; no other colour forms as seen at Palau (Marsh, 1977) were observed.

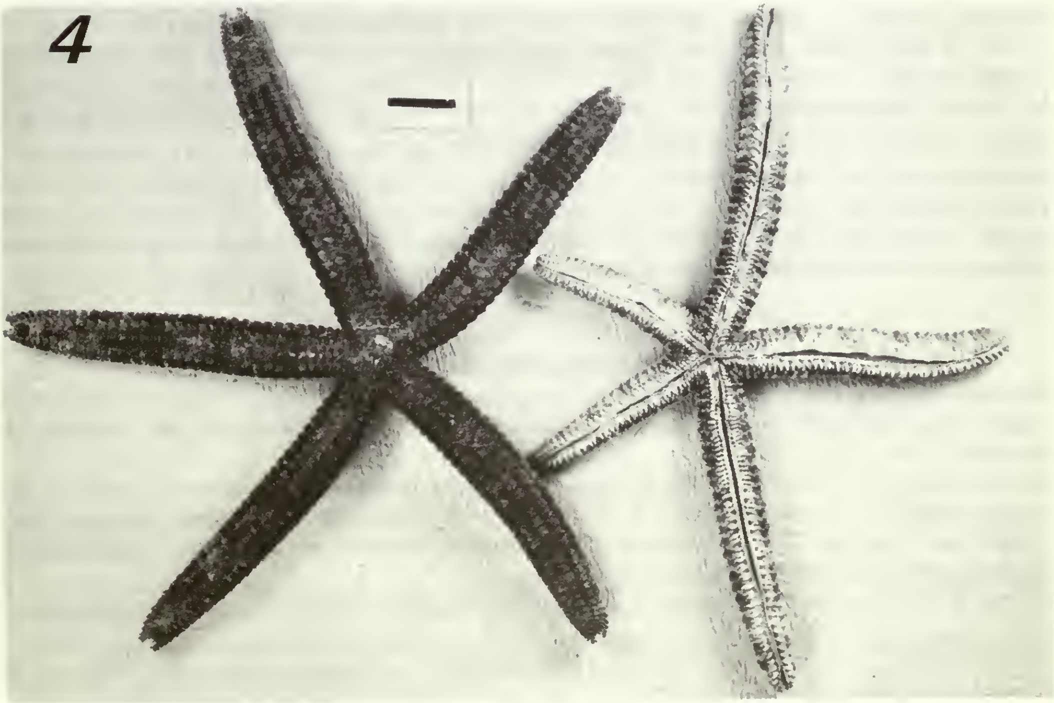
Hughes & Gamble (1977) list this species but their specimen came from grass beds in Passe Houareau (316–120) and we think it may instead have been *L. multifora*.

Linckia multifora (Lamarck, 1816)
See: Jangoux, 1973*a* : 32; Rideout, 1978 : 287 (asexual reproduction).
Abundant on coral rubble and sand among patch reefs in the Main Channel drainage system of the lagoon (120–080). One particular patch reef which consisted mostly of *Acropora acuminata* Verrill, a species new to Aldabra (B. Rosen, pers. comm.), had densities of 2–3 *L. multifora* per m^2 (R = 114 mm maximum). In the same habitat were found extreme densities of the holothurian *Stichopus chloronotus* Brandt of up to 12 per m^2, although their usual density was around 2 per m^2. Elsewhere in the lagoon *L. multifora* was found under boulders around Ile Esprit (114–063), beneath *Porites* and *Goniastrea* microatolls in Passe Houareau (316–120), among algae in north

3



4



Figs 3, 4 *Ophidiaster hemprichi* Müller & Troschel and *Dactylosaster cylindricus* (Lamarck), each viewed from above and below. (Scale = 10 mm.)

and south lagoon shores. Less common on seaward coasts but present on the algal covered sublittoral fringe on the south coast at Dune Jean Louis (275–039) and near Point Hodoul (407–080) and on the north coast at Anse Malabar (241–127).

Some specimens were infested with the parasitic gastropod *Thyca crystallina* (Gould, 1846).

Colour in life: pale flesh tone with numerous purple blotches and pale blue arm tips.

Nardoa sp.
Reported only by Price (1971 : 169) from the grass beds of the West Channels. The identification, however, was made in the field by another worker and may not be reliable.

Neoferdina offreti (Koehler, 1910)
See: Jangoux, 1973*b* : 778; Marsh, 1977 : 263.
Two specimens (R = 25·5 & 31 mm) were found on coral 1·0 m deep at low tide along the sides of the drainage channels of Main Channel in the lagoon (104–119) (108–120); another (R = 28·5 mm) was found on coral in 15 m off the research station (052–091).

Colour in life: disc centre pink, some plates with large violet spots, the rest off-white, pink below.

Ophidiaster hemprichi Müller & Troschel, 1842 Fig. 3
See: de Loriol, 1885: 22 (as *O. purpureus* Perrier); A. M. Clark & Rowe, 1971 : 61.
Fairly common under boulders over coarse rubble (range of R = 23–45 mm for 9 specimens) at the lower eulittoral off the research station (054–091); in similar microhabitats of the seaward platforms at Passe Gionnet (140–125) and Anse Malabar (241–127).

Colour in life: burgundy with irregular white flecking.

The considerable similarity of appearance of this species and *Dactylosaster cylindricus* prompted a suspicion that the two may represent growth stages of a single species. The skin of *D. cylindricus*, however, is obvious and shiny even in the dried specimens whereas the skin of *O. hemprichi* is not evident. Both have coarse granulation in the middle of the arm plates but in *O. hemprichi* this is surrounded by fine interstitial granulation rather than the thick skin of *Dactylosaster*. Both species are also sympatric in Mauritius from which a small specimen of undoubted *D. cylindricus* exists in the BMNH collections.

Tamaria lithosora H. L. Clark, 1921
See: H. L. Clark, 1921 : 90.
Reported only by Hughes & Gamble (1977). Listed as coming from a thick stand of *Halimeda* on the west side of Passe Houareau (316–119).

ASTEROPSEIDAE

Asteropsis carinifera (Lamarck, 1816)
See: de Loriol, 1885 : 67 (as *Gymnasteria carinifera* (Lamarck)); A. M. Clark, 1967 : 37; A. M. Clark & Rowe, 1971 : 65.
Quite common (R = 20·5–68 mm for 11 specimens) under boulders over rubble or gravel in the lower eulittoral of the seaward platform off the research station (054–091), Passe Gionnet (140–125) and Anse Malabar (241–127). Also found in heads of *Porites nigrescens* Dana from the lagoon grass flats (068–083) near West Channels.

Colour in life: pale grey with irregular green marking; always red-brown after preservation.

ASTERINIDAE

Asterina burtoni Gray, 1840
See: James & Pearse, 1969 : 84; A. M. Clark & Rowe, 1971 : 68; Achituv, 1969 : 329 (reproduction & distribution).
Fairly common (R = 3–13 mm for 7 specimens) in heads of *Porites* and *Acropora* in the lagoon (068–083, 120–080, 115–067). Individuals with 6–7 arms were the most common. Also recorded from the bases of *Thalassia* on lagoon grass flats (063–089), associated with the algal mat on the

sea-grass of this area, and under boulders on the seaward platform off the research station (054–091) and West Channels (060–070 to 060–090).

Dr Humphreys' specimens include 5 five-armed ones and 25 fissiparous multiradiate or newly-divided ones with up to 8, usually 7 arms. The maximum R is 7·5 mm. The spinelet form appears similar in the two lots of specimens, the abactinal ones slightly more elongate and tapering than in Red Sea individuals (see Clark & Rowe, 1971, fig. 17a), more like those of the specimen from Lord Howe Island, Australia (fig. 17g), usually with only three points at the tip. However, it is notable that the five-armed specimens have no more than three furrow spines, whereas the multiradiate ones of similar size have four or sometimes five.

It needs to be emphasized that the two syntypes of *A. burtoni* are either fissiparous (the six-armed one) or potentially so (the five-armed one), since both have multiple madreporites. Use of the name *A. wega* Perrier for fissiparous Red Sea specimens is therefore untenable since that must be a synonym of *A. burtoni*. If any second name should be needed for five-armed specimens with single madreporites from this area having squat abactinal spinelets (as opposed to the attenuated spinelets of *A. burtoni cepheus* Müller & Troschel), then a new name must be proposed.

ACANTHASTERIDAE

Acanthaster planci (Linnaeus, 1758)

See: H. L. Clark, 1921 : 101; Sale *et al.*, 1976 (review of biology); Yamaguchi, 1977*b* : 283 (zoogeography).

Found on coral in the lagoon from: West Channels (060–070 to 060–090), nearby grass (068–023), and along the edges of the Main Channel drainage system (104–110) (108–120) where it could be quite common. Found on coral off the seaward platform of the west coast (052–091) and the north coast at Passe Gionnet (140–125) where it was very common.

Colour in life: reddish-brown.

MITHRODIIDAE

Mithrodia clavigera (Lamarck, 1816)

See: Marsh, 1977 : 276.

Two specimens (R = 89·5 & 91 mm) were found under boulders over rubble at the lower eulittoral off the research station (054–091), another was among coral and sponge in Passe Femme (060–087), and one under a boulder in *Thalassodendron* in Passe Houareau (316–120). Unpublished BMNH records included a specimen from Mahé, Seychelles.

Colour in life: pale flesh tone with large brick-red patches, especially proximally, arm tips black.

Subclass **OPHIUROIDEA**

Note: all measurements are of dried specimens and thus the discs in particular are likely to be smaller than they would be in life. Abbreviations: d.d. = disc diameter; a.l. = arm length.

OPHIOMYXIDAE

Ophiomyxa australis Lütken, 1869 Figs 5, 6

See: Devaney, 1974 : 115.

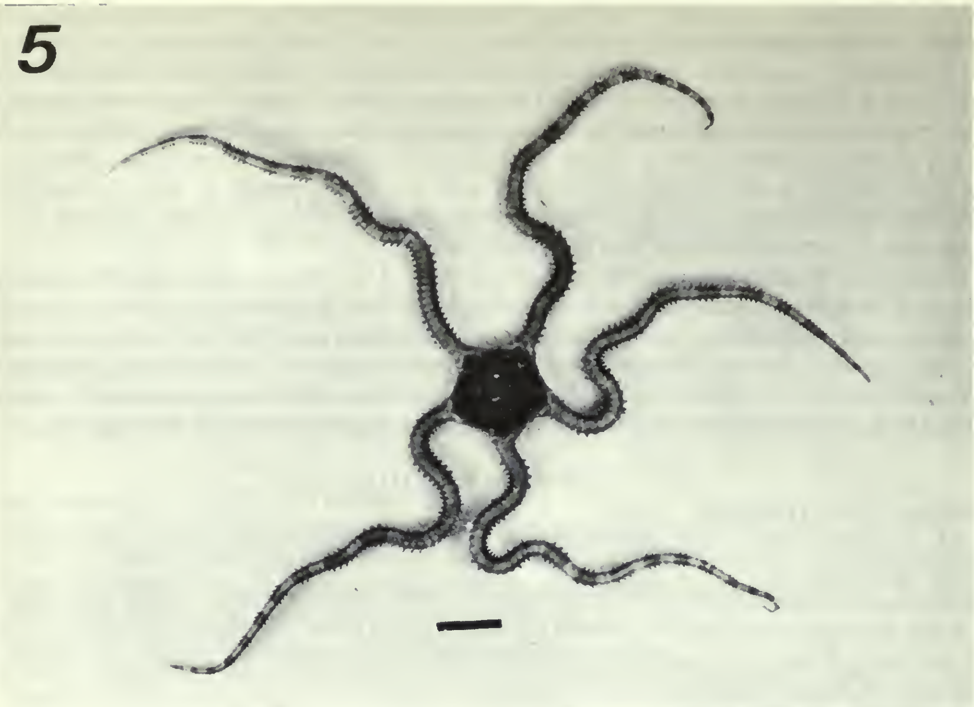
All 6 specimens (maximum d.d. = 23 mm; mean a.l. : d.d. = 4·9 : 1) were found under *Porites* microatolls in the lagoon grass flats (068–083) near West Channels.

With the exception of the oral papillae the whole animal is covered with smooth skin. In life the disc is very soft and amorphous.

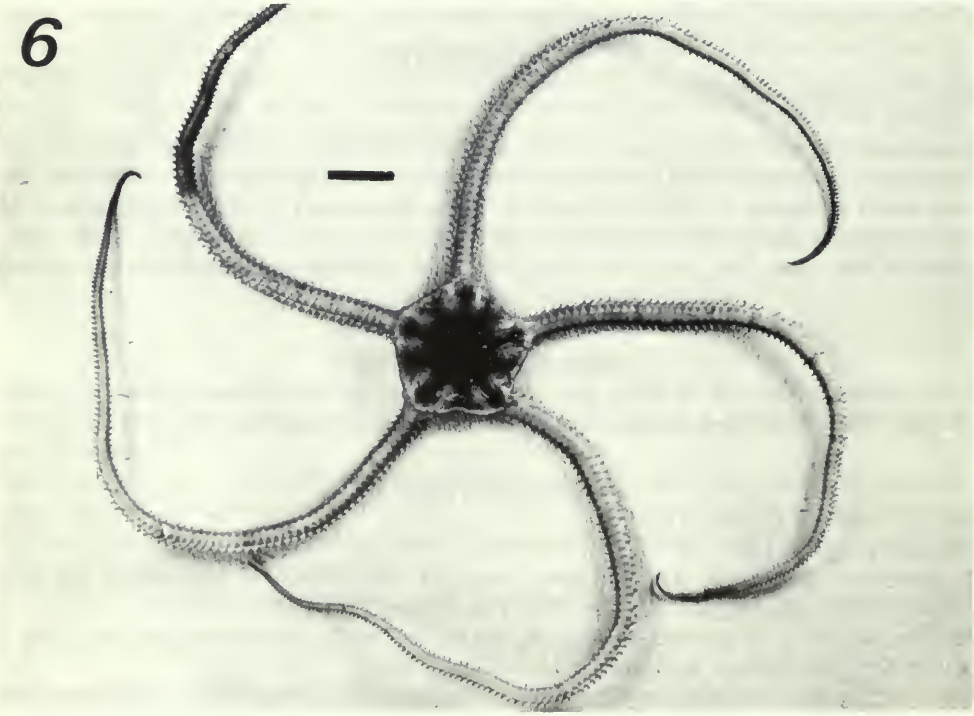
Colour in life: ranging from uniform light orange to uniform blood-red to disc blood-red with arms distally banded with yellow, in fact similar to that of two specimens collected by Dr M. Yamaguchi from Palau, Caroline Islands (BMNH reg. nos. 1975.11.25.45, 46).

One Aldabra specimen had on its disc an undescribed parasitic gastropod species of the genus *Hemiliostraca* Pilsbry, 1917 (A. Warén, in preparation). This is the first recorded host for this group of Eulimacea.

5



6



Figs 5, 6 *Ophiomyxa australis* Lütken, red specimen with banded arms and uniform orange-coloured specimen. (Scale = 10 mm.)

AMPHIURIDAE

Amphiodia (*Amphiodia*) *dividua* Mortensen, 1933
See: Mortensen, 1933 : 176; Cherbonnier & Guille, 1978 : 92–93, fig. 41.
Taken from under, as well as in, coral alongside and at the bottom of Passe Dubois (060–080).

Range extended from the Mascarene Islands and Madagascar.

Amphioplus (*Amphioplus*) *impressus* (Ljungman, 1867)
See: A. M. Clark, 1970 : 63; Cherbonnier & Guille, 1978 : 60–62, fig. 23.
Coral crypto- and infauna along both sides of Passe Dubois from *Thalassodendron* flats.

Range extended from Madagascar and the western Pacific.

Amphioplus (*Lymanella*) *hastatus* (Ljungman, 1867)
See: H. L. Clark, 1939 : 75; A. M. Clark & Rowe, 1971 : 102.

Reported by Hughes & Gamble (1977) only. Listed as coming from grass flats in the lagoon (063–089) near West Channels.

If correct, this would extend the range from East Africa and Madagascar.

Amphioplus (*Lymanella*) *integer* (Ljungman, 1867)
See: Balinsky, 1957 : 11; Cherbonnier & Guille, 1978 : 86–87, fig. 38.
Coral crypto- and infauna along the edges of Passe Dubois (060–080) in the *Thalassodendron* flats

Range extended from East Africa and Madagascar.

Amphipholis squamata (Delle Chiaje, 1829)
See: Devaney, 1974 : 125; Hughes & Gamble, 1977 : 335 (microhabitat information).
Mentioned in Hughes & Gamble (1977) as coming from numerous sites and listed in their appendix from Passe Houareau (315–118) (319–119), the seaward platform off West Channels (056–090), in the lagoon (060–089) near West Channels and the seaward platform of Anse Malabar (241–127). Particularly abundant in sheltered muddy habitats and associated with dense algal turf on sea-grass in sheltered habitats of these areas. Also found in the sediments of land-enclosed tidal pools at the eastern end of Ile Malabar (297–118) and Ile Picard (059–094).

We agree with Hughes & Gamble (1977) on the abundance of this ubiquitous little species of sheltered shores.

Amphiura (*Amphiura*) *inhacensis* Balinsky, 1957
See: Balinsky, 1957 : 11.
Infauna taken from boulders and dead coral heads in the lower eulittoral off the Settlement (055–108).

Range extended from Inhaca Island, southern Mozambique.

OPHIACTIDAE

Ophiactis picteti (de Loriol, 1893*a*)
See: A. M. Clark & Rowe, 1971 : 104; Cherbonnier & Guille, 1978 : 123–125, fig. 56.
Associated with sponge in the bases of heads of *Porites nigrescens* and *Millepora exacea* Forskaal from lagoon grass flats (068–083) near West Channels. Common in dead coral boulders at the seaward end of Passe Dubois (060–080); d.d. up to 6·1 mm.

Colour in life: disc uniformly brown or with irregular brown markings on white, arms banded white and brown with some dark spots on the white bands, ventrally the disc and arms white.

This is an extension of range from Madagascar and from Amboina, Indonesia – the type locality. Additionally, several specimens from Watamu, southern Kenya and the Pemba Channel, Tanzania, collected by W. F. Humphreys, are referable to this species. These, with the Aldabra specimens, were initially determined as *Ophiactis hemiteles* H. L. Clark (type locality Torres Strait) following Balinsky's record from Inhaca, Mozambique. However, the presence of only six, rarely seven, arm spines at d.d. 5 mm, rather than seven or eight and the markedly truncated form of all but the uppermost spine, with the tip more or less bihamulate, does not agree with H. L. Clark's description of the spines of *hemiteles* as sharp. Also these specimens from the western Indian Ocean all have a narrow median distal lobe to the oral shields, which H. L. Clark describes as simply elliptical in *hemiteles*.

In the key given in Clark & Rowe, 1971, *O. picteti* (with *O. sinensis* Mortensen) and *O. hemiteles* were poorly distinguished by the adoral shields being relatively large and interradially contiguous only in *hemiteles*, the shields of *picteti* being obscured by skin. In the present specimens the skin is sufficiently transparent to show the limits of the shields, which are rather variable in extent interradially; even in the same specimen some may be contiguous while others are not. Nor is the relative arm length reliable in distinction. The arms were broken in the holotypes of both species. The estimates of their length against d.d. were given as ×8 for *hemiteles* and ×6 for *picteti* but de Loriol noted that his estimate of the arm length was very approximate. The arms are broken in most of the present specimens but a small one has a.l. 33 mm, d.d. 3·5 mm, a ratio of 9·4/1; in another of similar size it is 8·4/1. One unusual feature that they show is a pair of slight longitudinal grooves on each ventral arm plate, just as in de Loriol's fig. 2b (1893*a*) from the holotype of *O. picteti*. This character in conjunction with the blunt arm spines supports recognition of the Aldabra and East African material as *O. picteti* rather than *O. hemiteles* and is in accord with the identification by Cherbonnier & Guille (1978) of a malagasy specimen as *O. picteti*.

It may be noted that preserved specimens with the colour muted have considerable resemblance to the occasional five-armed specimen of *Ophiactis savignyi*, especially in the relatively large radial shields, two distal oral papillae each side of the jaw, elliptical dorsal arm plates and truncated rugose arm spines, also the light-coloured patch on the distal part of each pair of radial shields. However, the absence of the small median distal lobe on the dorsal arm plates (so characteristic of *O. savignyi*) and the isolation of the scales in the skin of the central part of the disc in specimens of *O. picteti* of d.d. more than *c.* 4·5 mm, should serve to distinguish them.

Ophiactis savignyi Müller & Troschel, 1842
See: Balinsky, 1957 : 14; A. M. Clark & Rowe, 1971 : 103.
Commonly found associated with sponge in the bases of heads of *P. nigrescens* and *M. exacea* from lagoon grass flats (068–083) near West Channels, extremely common on sponge on rubble in the central intake of the land-enclosed tidal pool on Ile Picard (059–094), common in the interstices of *Halimeda* in Passe Houareau (316–114), in algal mat and sea-grass bases in lagoon grass beds (063–089) near West Channels. A. l. max. = 15 mm; a.l. : d.d. = 4·7 : 1.

Colour in life: basically green, disc with fairly regular light and dark green markings, arms banded with light and dark green, ventrally disc and arms white with some distal green banding on the arms.

Ophiactis versicolor H. L. Clark, 1939
See: A. M. Clark, 1967 : 43 (as *Ophiactis carnea* but as *O. versicolor* in footnote).
Taken from coral along the edge of Passe Dubois (060–080) where it occurred as both coral crypto- and infauna.

Range extended from East Africa, Madagascar and the Mascarene Islands.

OPHIOTRICHIDAE

Macrophiothrix demessa (Lyman, 1861)
See: Devaney, 1974 : 139.
Occasionally found in or under *Porites* heads or microatolls in the lagoon grass flats (068–083) near the West Channels. D.d. max. = 12·5 mm; a.l. : d.d. = 11 : 1.

Colour in life very variable but not spotted like *M. longipeda* below.

Macrophiothrix longipeda (Lamarck, 1816)
See: Devaney, 1974 : 140.
Usually found as solitary individuals under boulders and coral heads over sand or sandy gravel with their arms extended upward along crevices in the covering rock or coral. Found in the lower eulittoral of wasted platforms off the research station (054–091), Anse Malabar (241–127) and near Pt Hodoul (407–080). Occurs sublittorally off the research station (052–091), in lagoon grass flats (068–083) near West Channels, Main Channel drainage area (108–120), and in Passe Houareau (316–119) associated with *Halimeda* besides coral heads and boulders. As growth proceeds, the

arm length increases in relation to the disc diameter, e.g. d.d. max. = 9·5 mm, a.l. : d.d. = *c.* 18 : 1; d.d. 17 mm, a.l. : d.d = 27 : 1.

Colour in life: bluish with dark blue spots, the spinose disc with large spotted radial shields, ventrally lighter blue with dark spots.

Ophiothrix (*Keystonea*) *propinqua* Lyman, 1861
See: Balinsky, 1957 : 21; A. M. Clark & Rowe, 1971 : 107.
Exceedingly common in coral heads with small interstitial spaces like *Millepora exacea* in the lagoon grass flats (068–083) near the West Channels. Also abundant in dead coral boulders as well as live coral in the West Channels (060–070 to 060–090), Main Channel drainage system (108–120), and Passe Houareau (316–120). D.d. max. = 8 mm, a.l. : d.d. = 8 : 1.

Colour in life: very variable as noted by Balinsky (1957) but overall dark bluish with darker arm banding.

Ophiothrix trilineata Lütken, 1869
See: Balinsky, 1957 : 30; Devaney, 1974 : 150.
Fairly common in heads of *Millepora* and *Porites* from lagoon grass flats (068–083) near West Channels, in coral in the Main Channel drainage system (108–120) of the lagoon and in coral along Passe Houareau (316–120). D.d. max. = 8 mm; a.l. : d.d. = 5 : 1.

Colour in life: disc always dark blue, arms basically blue or green with five characteristic median lines alternating white and dark blue; arm spines glassy, reddish and sometimes with a dark line, ventrally white overall.

Ophiothrix (*Acanthophiothrix*) *purpurea* von Martens, 1867
See: Devaney, 1974 : 141.
Commonly found epizoic on *Millepora tenera* Boschma from 5 to 30 m on the sides of Passe Dubois (160–180), along Main Channel drainage system of the lagoon (104–110), at 15–30 m off the research station (052–091), at 10–30 m off Passe Gionnet (140–125) and along Passe Houareau (316–120). D.d. max. = 7 mm; a.l. : d.d. = 9·5 : 1. Very delicate and difficult to collect intact. Much more common at night (Humphreys, pers. comm.).

Colour in life: disc patterned in red, arms dark red with narrow red median line outlined in white, arm spines red, ventrally lighter red with a dark median line along the arms.

Ophiothela tigris Lyman, 1871 Fig. 7
See: A. M. Clark & Rowe, 1971 : 116; A. M. Clark, 1976*a* : 111 (epizoic habits).
Epizoic on the stinging hydroid *Aglaophenia cupressina* Lamouroux, 1816 from the coral flats in the Main Channel drainage system of the lagoon (104–110); also found on heads of *P. nigrescens* and *M. exacea* in the lagoon grass flats (068–083) and near West Channels on coral along Passe Houareau (316–120). D.d. max. = 7 mm; a.l. : d.d. = *c.* 3·5 : 1 but relative arm length very variable.

Colour in life: disc rich green but centrally with pattern of black and yellow concentric markings within pentagonal outline, arms uniform green but spines distally white and proximally blue, ventral colour light blue overall.

OPHIOCOMIDAE

A more detailed account of the microhabitats of this family on Aldabra is given earlier (pp. 89–93), also a table summarizing the known associates of *Ophiocoma* species.

Ophiarthrum elegans Peters, 1851
See: H. L. Clark, 1921 : 139; Devaney, 1974 : 150.
Occurs in pools at the bases of *Thalassodendron* in rubble on the seaward platforms of the west (058–091) and north (241–127) coasts, under rubble in the lower eulittoral of these seaward platforms, under coral over sandy gravel in the lagoon grass flats (068–083) near West Channels, along Main Channel drainage system (108–120) and along Passe Houareau (316–120). D.d. max. = 22 mm; a.l. : d.d. = 4·5–9·5 : 1, the arms extremely variable in length.

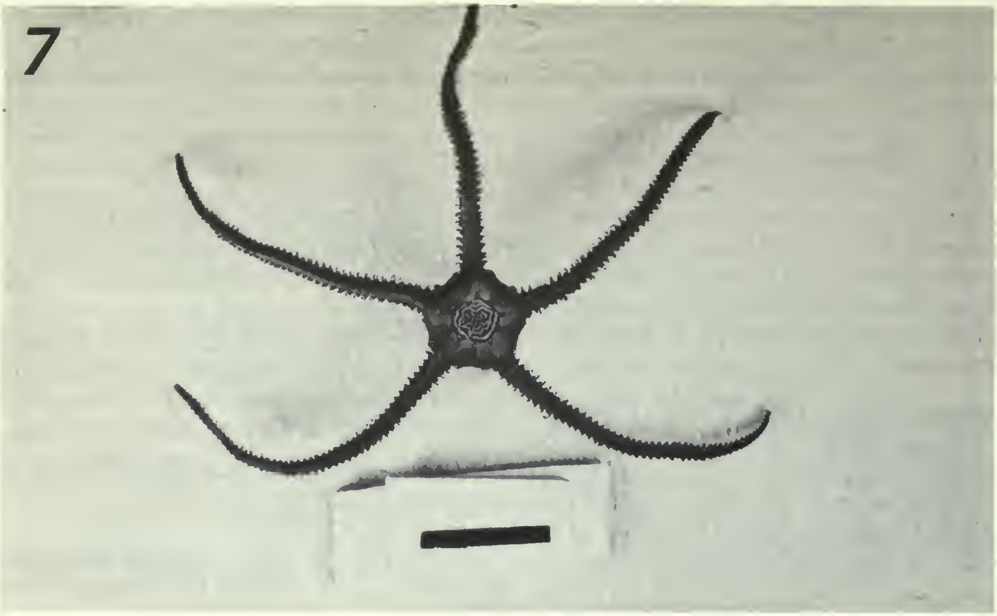


Fig. 7 *Ophiothela tigris* Lyman. (Scale = 10 mm.)

Colour in life: disc uniform black, arms pale cream with red bands always fading after preservation, arm spines pale cream with black spots sometimes forming irregular annulations, ventrally overall white.

Ophiocoma brevipes Peters, 1851
See: Devaney, 1974 : 151.
Prefers sandy substrates under boulders on seaward platforms of the west (058–091) and north (241–127) (360–112) coasts. Also found at the bases of *Thalassodendron* and *Halimeda* in these areas as well as Passe Houareau (316–120) and West Channels (060–070 to 060–090). D.d. max. = 19 mm; a.l. : d.d. = 3·6 : 1.

Colour in life: disc off-white with irregular green markings, arms off-white with pale green banding, ventrally off-white overall but sometimes stained by amber-coloured gut regurgitations.

Commonly found carrying the polychaete associate *Holopidella nigropunctata* (Horst, 1915), occasionally with *Gyptis* ? sp., and once with a specimen of *Lepidasthenia* sp. as well but this could have been only incidental (Dr P. E. Gibbs, pers. comm.).

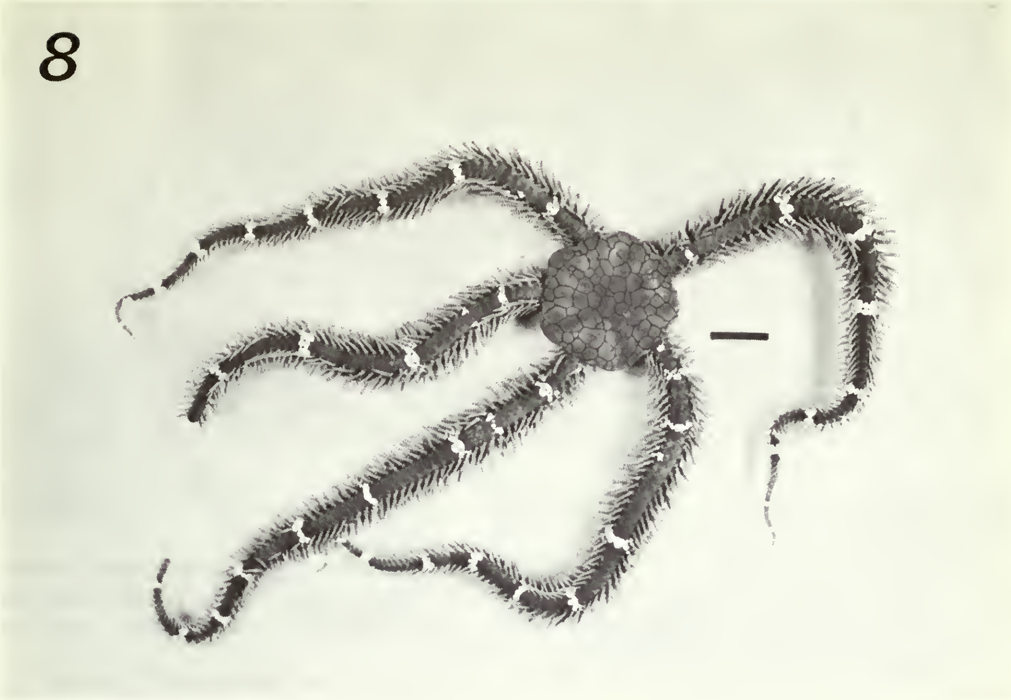
Ophiocoma doederleini de Loriol, 1899 Figs 8–10
See: Devaney, 1970 : 14; 1974 : 154.
Previously recorded from Aldabra as *Ophiocoma dentata* Müller & Troschel, 1842.

Fairly common under boulders over gravel and rubble and in the bases of *Thalassodendron* in the lower eulittoral of seaward platforms of the west (058–091) and north (241–127) coasts. More common in the shallow sublittoral under coral microatolls, especially *Porites*, over sandy gravel in lagoon grass beds (068–083) near West Channels and along Passe Houareau (316–120). D.d. max. = 27 mm; a.l. : d.d. = 4·2 : 1.

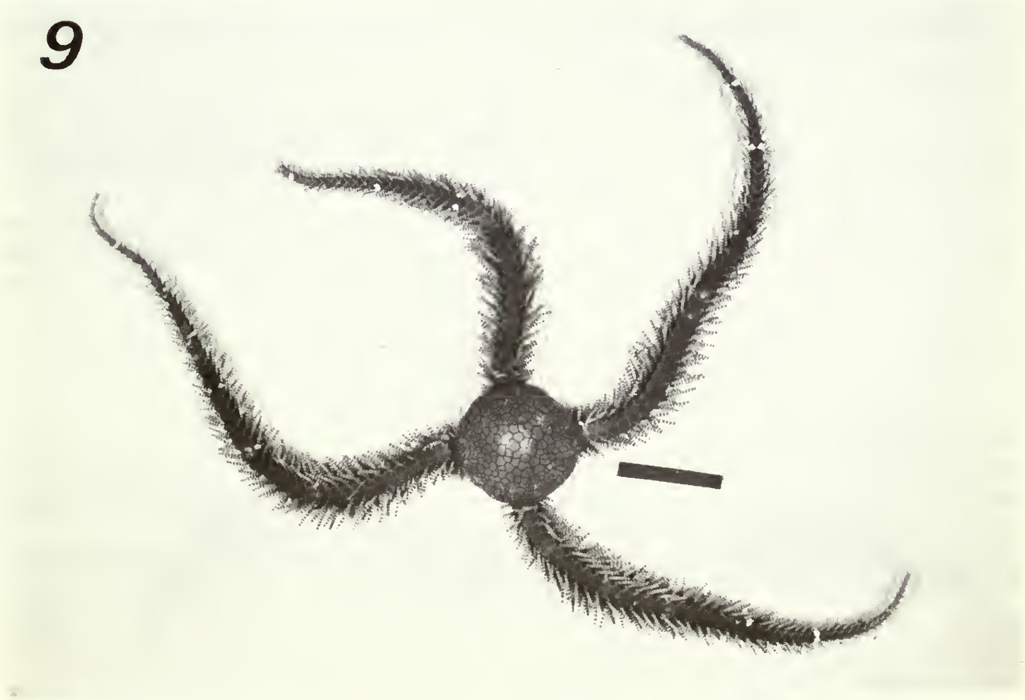
Colour in life: basically mid-grey, disc grey with fine black reticulating lines or, less commonly, with white-ringed black spots, or speckled with light spots, arms commonly with spotted white bands all the way round, arm spines always annulated white and grey, ventrally the same grey as dorsally, oral shields white peripherally with large irregular grey blotches.

Over 80% of all specimens were infested with the new pycnogonid species *Anoplodactylus ophiurophilus* Stock (1979). Some *O. doederleini* were found carrying the polynoid *H. nigropunctata*.

8



9



Figs 8, 9 *Ophiocoma doederleini* de Loriol, five- and four-armed specimens. (Scale = 10 mm.)

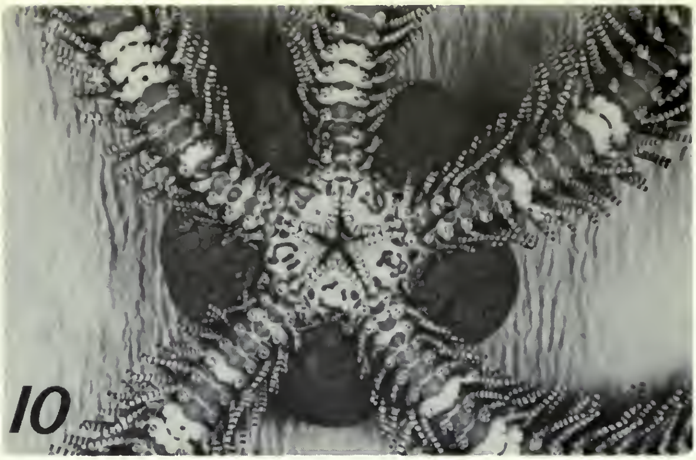


Fig. 10 *Ophiocoma doederleini*, detail of disc and arm bases, from below. (Scale = 10 mm.)

Ophiocoma erinaceus Müller & Troschel, 1842 Figs 11, 12
See: Devaney, 1974 : 155.
The most ubiquitous ophiocomid on Aldabra. Common in coral heads in all the channel areas of the lagoon and off the seaward platforms of the west and north coasts. Present on all the seaward platforms on all coasts of the atoll and particularly associated with rock and rubble rather than sandy substrates. D.d. max. = 30 mm; a.l. : d.d. = 4·5 : 1.

Colour in life: all black, some had ventral arm plates with some white trim, occasional individuals had bright orange podia.

The least infested of the three *Ophiocoma* species which bear the pycnogonid *A. ophiurophilus*.

Ophiocoma pica Müller & Troschel, 1842
See: Devaney, 1970 : 25; 1974 : 159.
Found in coral like *O. erinaceus*, but less commonly, wherever coral was found in the lagoon channel areas or off the seaward platforms on the west and north coasts. Not common in the eulittoral under rubble. D.d. max. = 18 mm; a.l. : d.d. = 4·0 : 1.

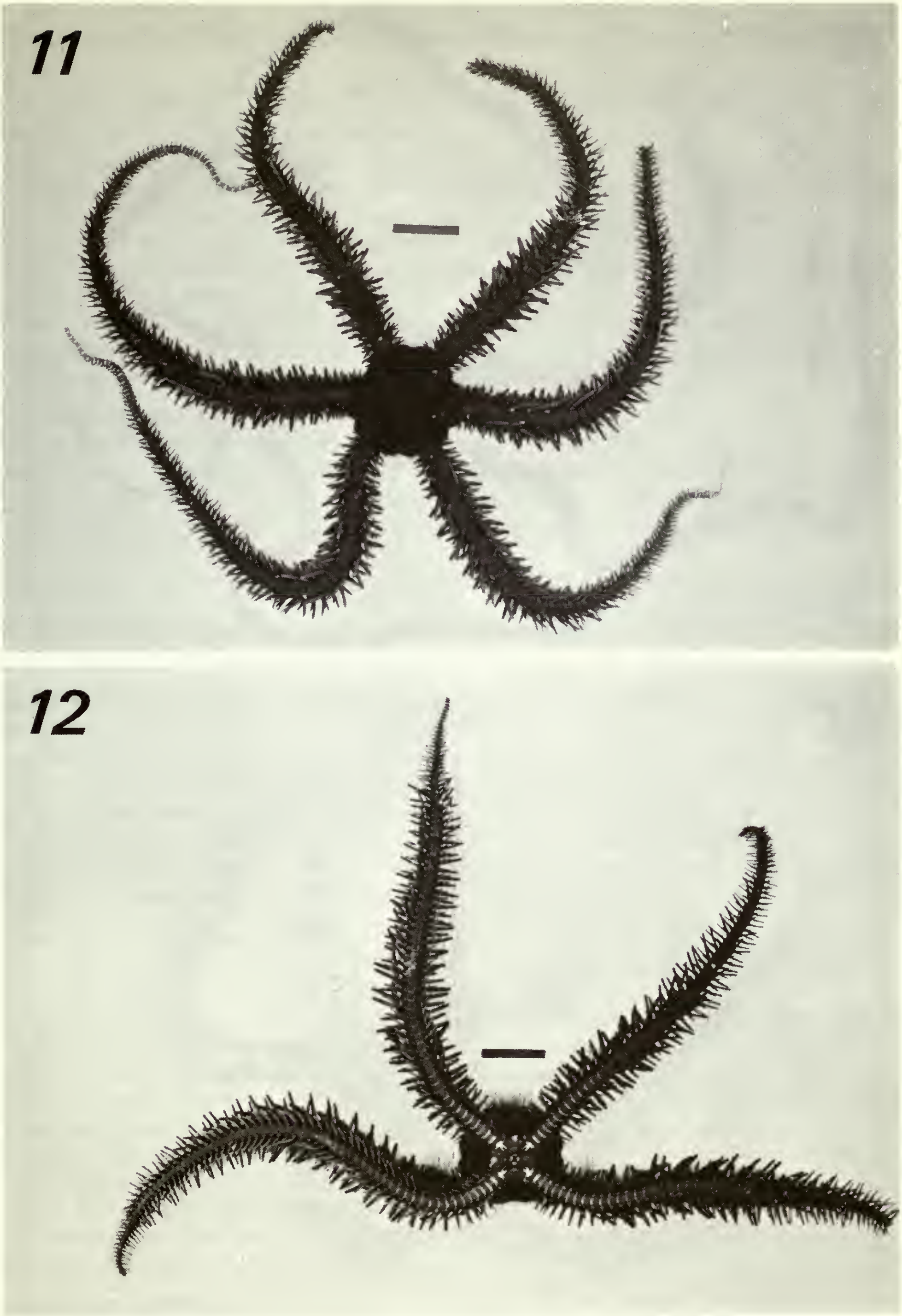
Colour in life: disc with thin gold radiating lines on a dark brown background, long dark brown arm spines, dumb-bell-shaped gold and cream bands on the dorsal arm plates which were otherwise dark brown, ventral arm plates with a similar pattern, oral shields dark brown with white lateral edges.

This species has an infestation level by *A. ophiurophilus* between that of *O. doederleini* and *O. erinaceus*.

Ophiocoma pusilla (Brock, 1888)
See: Devaney, 1970 : 25; 1974 : 160.
Common in the lower eulittoral under rubble on the coastal platforms of the west and north coasts, under coral heads of lagoon grass beds (068–083) near West Channels, Passe Houareau (316–120) and Main Channel (108–120). D.d. max. = 7 mm; a.l. : d.d. = 2·7 : 1.

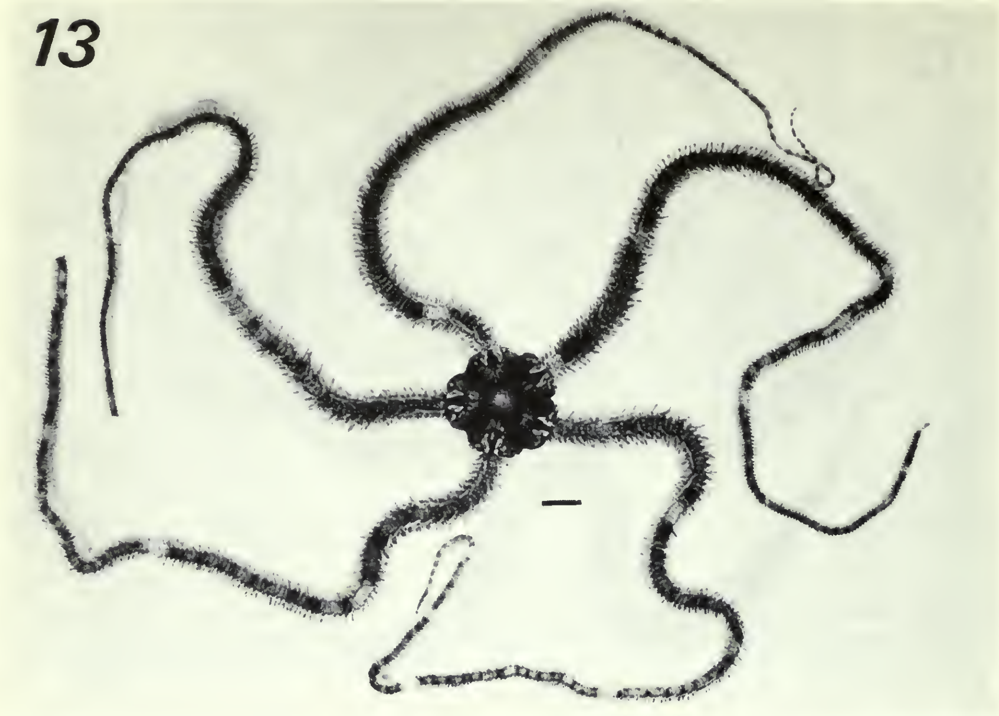
Colour in life: disc uniform dark brown, occasionally spotted with white-rimmed dark spots, arms dark brown with lighter banding, ventrally overall red-brown.

Ophiocoma scolopendrina (Lamarck, 1816) Fig. 13
See: Devaney, 1974 : 161.
Externally common in the upper eulittoral zone of all rocky seaward shores around the atoll. Uncommon in grass beds of seaward and lagoon platforms or in lower eulittoral or shallow sublittoral. Common around the bases of lagoon islets. With increasing size the arms become relatively longer, e.g. d.d. = 13·4 mm; a.l. : d.d. = 4·6 : 1; d.d. = 27 mm; a.l. : d.d. = 6·0 : 1; d.d. = 29 mm, a.l. : d.d. = 10·2 : 1.

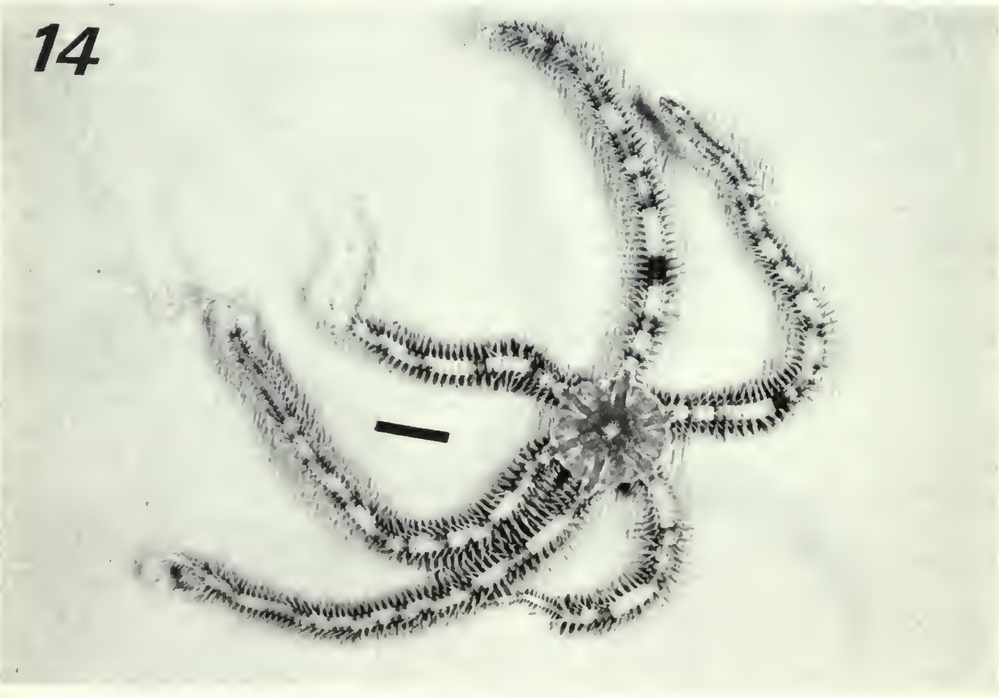


Figs 11, 12 *Ophiocoma erinaceus* Müller & Troschel, six-armed specimen from above and four-armed specimen from below. (Scale = 10 mm.)

13



14



Figs 13, 14 *Ophiocoma scolopendrina* (Lamarck) and six-armed specimen of *O. valenciae* Müller & Troschel. (Scale = 10 mm.)

Colour in life: patterns extremely variable, disc usually dark with irregular off-white markings, dorsal arm plates brownish with irregular distal white spots, arm spines sometimes annulated, sometimes spotted, sometimes orange-tipped, ventrally overall off-white, oral shields occasionally with grey blotches.

Occasionally white triclads were found on the ventral sides of specimens.

Ophiocoma valenciae Müller & Troschel, 1842 Fig. 14
See: H. L. Clark, 1921 : 131; Devaney, 1970 : 29.
The dominant echinoderm at the bases of *Thalassia* that is heavily covered with algal mat, among which *Halimeda* and *Gracilaria* is prominent. Such habitats occurred on sheltered grass beds that never completely dried at low tide in the lagoon (065–090) near West Channels and Passe Houareau (316–118). Rarely found in lower eulittoral of seaward platforms or in shallow sublittoral under coral. D.d. max. = 22 mm; a.l. : d.d. = 5·5 : 1.

Colour in life: disc uniform dull green, arms dull green with occasional darker banding, arm spines dull green, ventrally overall pale green. During preservation the green colouration usually turns a light tan brown.

Ophiocomella sexradia (Duncan, 1887)
See: A. M. Clark & Rowe, 1971 : 99 & 118; Devaney, 1974 : 162.
Not too common as coral-head infauna of *P. nigrescens* and *M. exacea* from the lagoon grass flats (068–083) near West Channels, in sea-grass bases and coral along Passe Houareau (316–118). May be a sponge associate like the similarly fissiparous and usually six-armed *Ophiactis savignyi*. D.d. max. = 4 mm; a.l. : d.d. = 3·8 : 1.

Colour in life: disc dark green, arms dark green with light green banding, ventrally paler green overall.

This confirms the unspecified extension of range noted in A. M. Clark & Rowe (1971 : 86) to the islands of the western Indian Ocean from East Africa and Madagascar.

Ophiomastix caryophyllata Lütken, 1869 Fig. 15
See: H. L. Clark, 1921 : 137; A. M. Clark & Rowe, 1971 : 120.
Common in coral heads in all the channel areas of the lagoon and off the seaward platforms of the west and north coasts. More abundant even than *O. erinaceus* under *Porites* microatolls on the lagoon grass flats (068–083) near West Channels. D.d. max. = 19 mm; a.l. : d.d. = 7·0 : 1.

Colour in life: the spiny disc white with large dark purple spots outlined with white, both basal and ventral arm plates with a distal V-shaped white band superimposed on dark purple, oral shields outlined white with a central labyrinthine purple design.

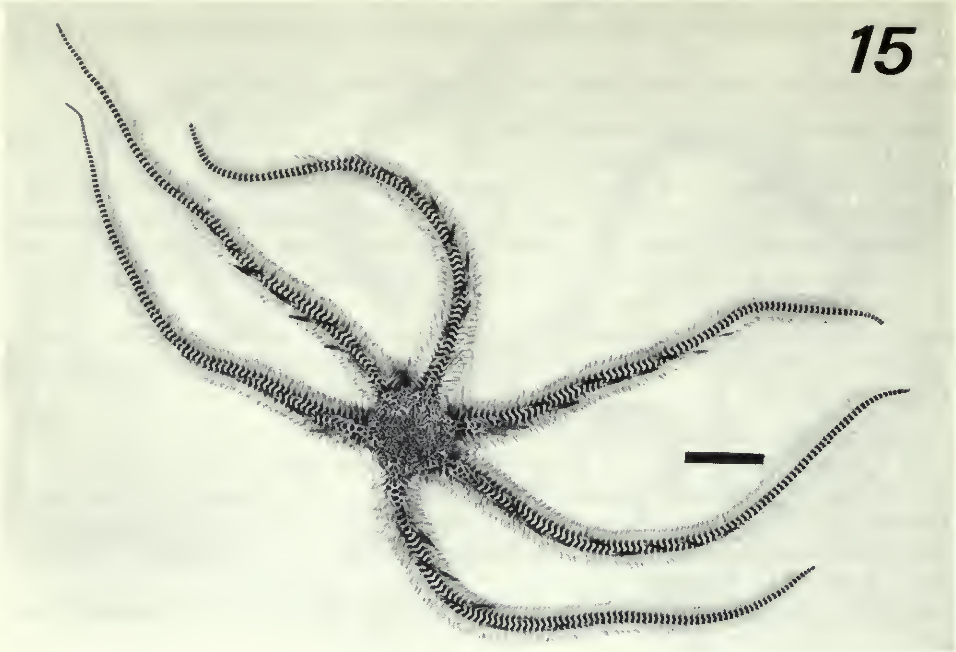
Ophiomastix koehleri Devaney, 1977 Fig. 16
See: A. M. Clark & Rowe, 1971 : 118 (as *Ophiocoma wendti*: Koehler); Devaney, 1977 : 275; Cherbonnier & Guille, 1978 : 186–188, pl. 11, figs 1, 2.
Previously recorded from Aldabra as *Ophiocoma wendti* : Koehler by Hughes & Gamble (1977).

One specimen only, found under a *Porites* microatoll over sandy gravel in the lagoon grass beds (068–083) near West Channels. D.d. = 15 mm; a.l. = 106 mm; a.l. : d.d. = 7·0 : 1.

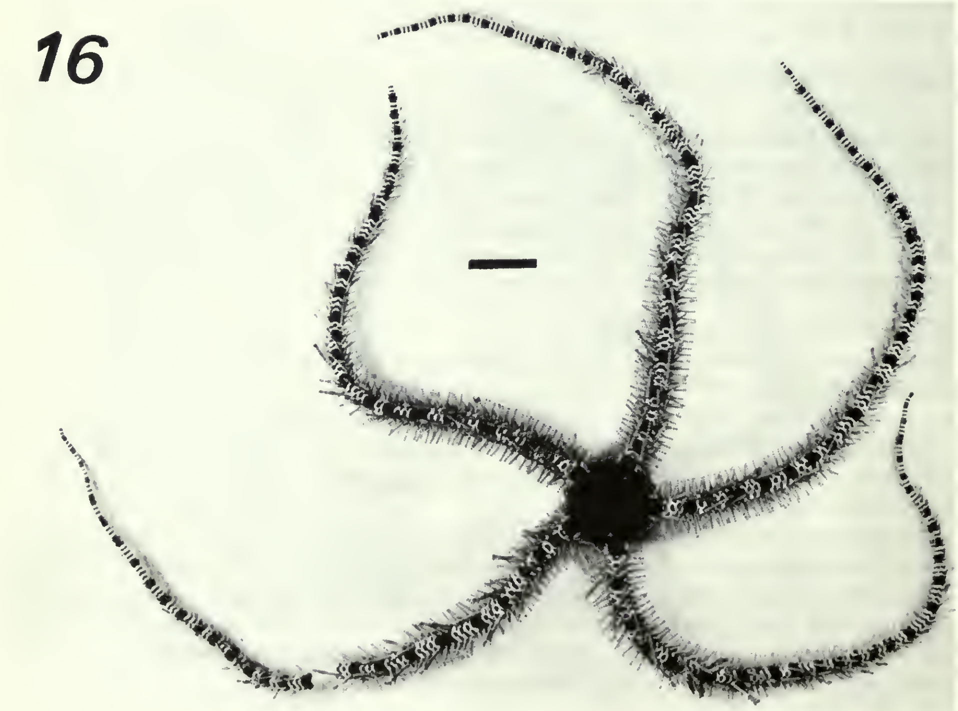
Colour in life: the spineless disc uniform dark purple with white-marked edges, dorsal arm plates basically white with large irregular purple blotches which may occupy most of the plate so that about two consecutive segments out of five are almost completely dark, forming an arm band, large dorsal clavate arm spines pale purple or mottled, small arm spines annulated white and purple, ventral arm plates white with large proximal purple blotches that can occupy almost the whole plate in positions corresponding to the dark areas dorsally, tentacle scales banded, oral shields with large dark purple blotches, podia red.

Ophiomastix venosa Peters, 1851
See: H. L. Clark, 1921 : 138.
Not common; under boulders, coral heads, and *Porites* microatolls in the lagoon grass beds (068–083) near West Channels, along Passe Houareau (316–118), in depression at cliff base of Anse Malabar (241–127), seaward platform of the south coast when it occurred under boulders

15



16



Figs 15, 16 *Ophiomastix caryophyllata* Lütken and *O. koehleri* Devaney. (Scale = 10 mm.)

(345–037). D.d. max. = 41 mm; a.l. : d.d. = 5·5 : 1, the ratio not increasing with absolute disc size.

Colour in life: basically bright yellow, the almost completely spineless smooth disc yellow with dark lines outlined in white, arm spines, including the enlarged clavate upper ones, yellow with a dark line, dorsal arm plates with an ill-defined darker yellow median band, ventrally pale yellow overall, podia yellow.

OPHIONEREIDIDAE

Ophionereis dubia (Müller & Troschel, 1842)
See: A. M. Clark & Rowe, 1971 : 122.
Recorded by Hughes & Gamble (1977) and listed as common in a thick stand of *Halimeda* in Passe Houareau (316–117) and from dense *Thalassia* on the west coast seaward platform (056–090). Specimens of confirmed identity have been found in and under coral along the edge of Passe Dubois (060–080). Owing to poor preservation, no measurements or colour notes can be given.

Range extended from East Africa, Madagascar and the Mascarene Islands.

Ophionereis porrecta Lyman, 1860
See Devaney, 1974 : 174.
Fairly common in the crevices of boulders in the lower eulittoral of the west and north coast seaward platforms, in heads of *P. nigrescens* and *M. exacea* from lagoon grass flats (068–083) near West Channels, in heads of *Millepora platyphylla* Ehrenberg from the bottom of Main Channel. D.d. max. = 15 mm; a.l. : d.d. = 9·0 : 1.

Colour in life: disc greyish with irregular dark markings, the dark pattern much more prominent in young specimens, arms mottled white and grey with dark spots, the short spines white, ventrally white with grey blotches overall.

OPHIODERMATIDAE

Ophiarachna affinis Lütken, 1869 Figs. 17, 18
See: A. M. Clark & Rowe, 1971 : 123; Devaney, 1974 : 175.
One specimen found under a *Porites* microatoll over sandy gravel in lagoon grass flats (068–083) near West Channels.

Colour in life: strongly resembling that of *Ophiocoma doederleini*, basically mid-grey, disc light grey with widely-spaced black spots and a pale ramifying linear pattern, arms mid-grey with white bands, arm spines annulated white and grey, including the elongated ventralmost spines, ventrally mid-grey, oral shields white with irregular grey markings. The overall impression is that this specimen is less robust in construction than *O. doederleini*. D.d. = 25 mm; a.l. = 97 mm; a.l. : d.d. = 3·9 : 1.

Range extended from Indonesia.

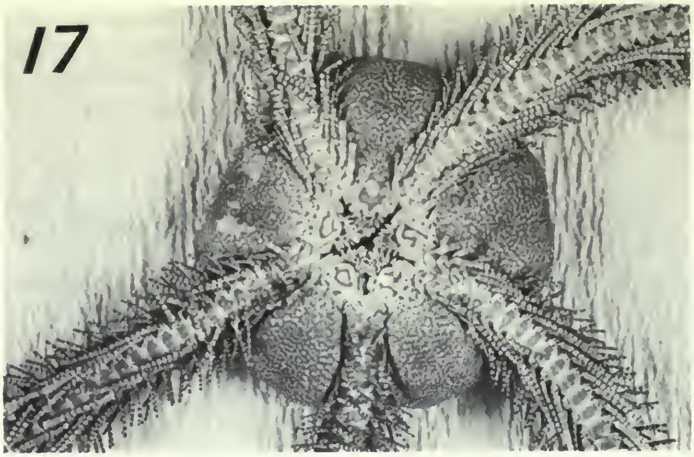
Ophiarachnella gorgonia (Müller & Troschel, 1842)
See: H. L. Clark, 1921 : 141; A. M. Clark & Rowe, 1971 : 125.
Three specimens found under *Porites* microatolls over sandy gravel in the lagoon grass flats (068–083) near West Channels. D.d. max. = 21 mm; a.l. : d.d. = 5·1 : 1.

Colour in life: disc off-white with irregular light brown markings, radial shields mottled white and grey with small black spots, arms off-white with mid-brown bands one to three segments wide, ventrally overall off-white with arms darker distally.

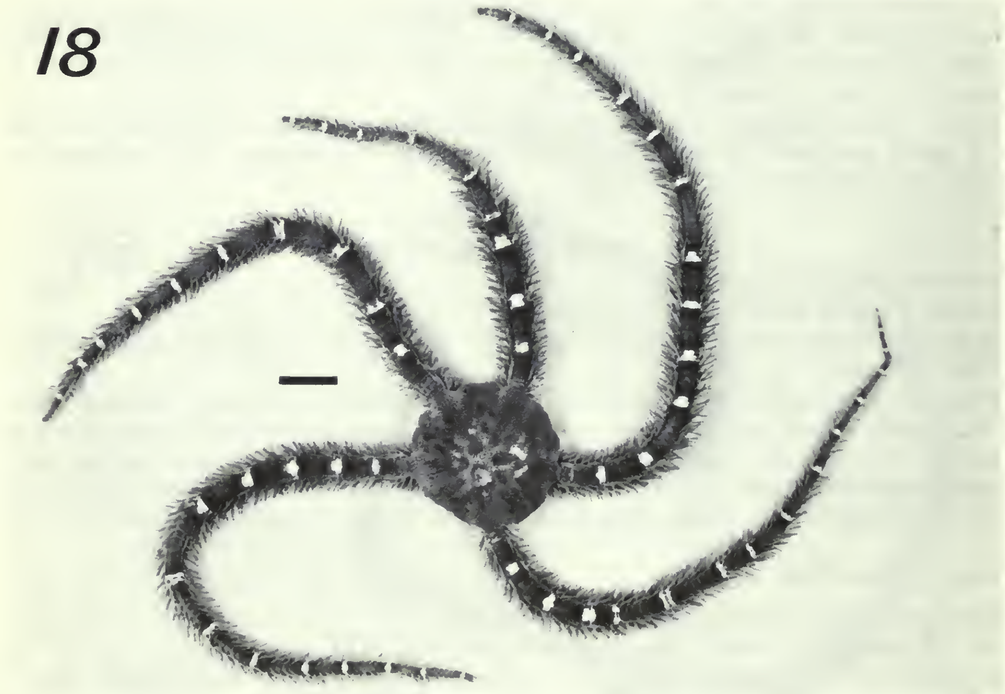
Ophiarachnella macracantha aldabrensis **subsp. nov.** Figs 19–21
See: H. L. Clark, 1909 : 126; A. M. Clark & Rowe, 1971 : 126 (for *O. macracantha*).
Holotype: B.M. reg. no. 1978.9.1.1, from under a *Porites* microatoll over sandy gravel in the lagoon grass flats (068–083) near West Channels. D.d. = 19 mm, a.l. = 83 mm; a.l. : d.d. = 4·4 : 1.

Colour in life: disc blood-red with radial shields the same colour, arms basically blood-red with a lighter linear pattern distally, also with pale transverse bands superimposed on this distal linear pattern, ventrally the arms paler, oral shields not white, unlike the other specimens mentioned below, but with a very broad red band that may cover up to half the oral shield.

17



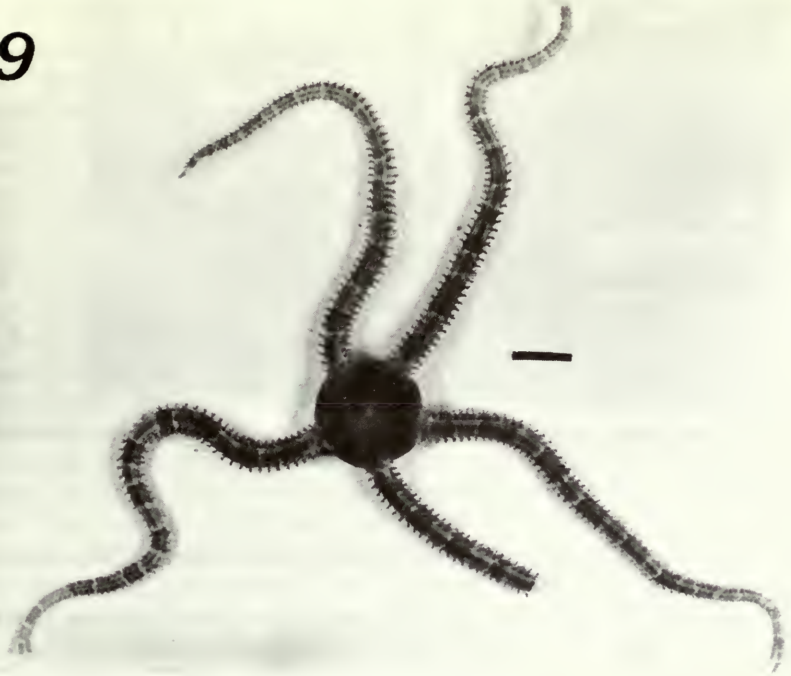
18



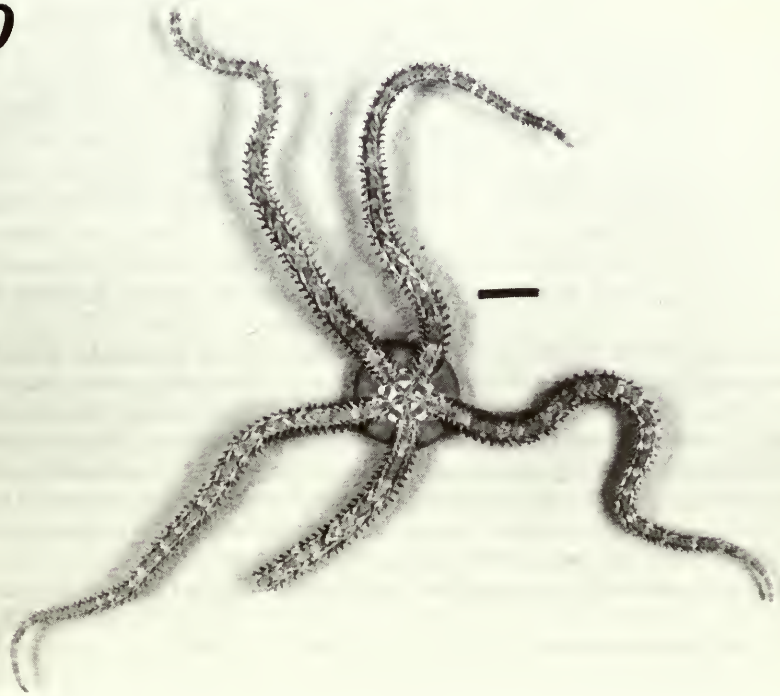
Figs 17, 18 *Ophiarachna affinis* Lütken, detail of disc and arm bases from below, whole animal from above. (Scale = 10 mm.)

This specimen, still vividly red after being dry for 6 months, was compared with two Pacific examples of *O. macracantha*, a dried one from Palau, western Caroline Islands, collected by Dr M. Yamaguchi, and a spirit specimen from Fiji, collected by the *Challenger* (named by Lyman *Pectinura rigida* – a synonym of the closely-related *O. septemspinosa* (Müller & Troschel)). Arm length/disc diameter in the two last is *c.* 100 mm/26 mm (=3·8/1) and 110 mm/21–22 mm (=5·1/1) respectively. Both have brown bands on the arms and the Palau specimen still has the disc pink and grey, as when first dried. The maximum arm spine number in the three specimens is 7, 8 and 9 respectively but the smaller number in the Aldabra specimen can be attributed to its smaller size. Its enlarged lowest arm spines are particularly flattened and spatulate in form, as

19



20



Figs 19, 20 *Ophiarachnella macracantha aldabrensis* subsp. nov. (Scale = 10 mm.)

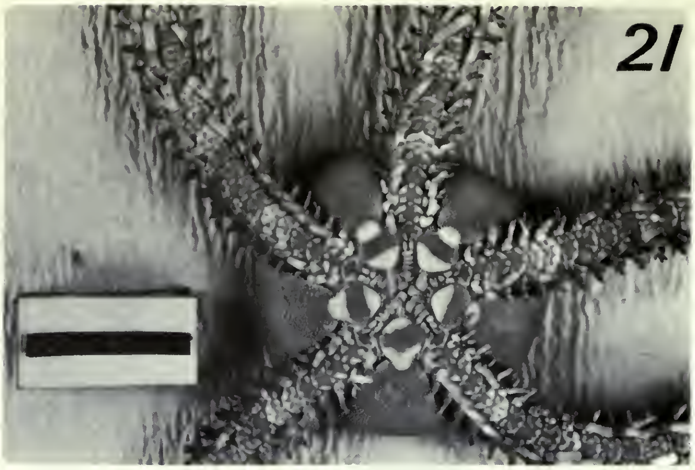


Fig. 21 *Ophiarachnella macracantha aldabrensis*, detail of disc and arm bases from below. (Scale = 10 mm.)

broad at the tip as the base, whereas in the Pacific specimens the tips are somewhat thickened (though not quite cylindrical) and more or less narrowed. The longest of these spines just exceed twice the segment length, equalling 3·0–3·5 mm. It should be noted in all the specimens that only one in every two or three of the lowest spines is markedly enlarged, a feature which was either overlooked by H. L. Clark or absent in the type material of *O. macracantha* from Ponape, eastern Carolines, where up to nine arm spines were found at R 24 mm. The enlarged spines mostly alternate on the two sides of every second (or sometimes third) segment from about segment eight onwards. The size of the disc granules and exposed parts of the radial shields and the structure of the jaws are similar in all three and the minor difference in shape of the arm spines seems to be the only morphological difference to support the vivid colouration in distinguishing the Aldabra specimen from the Pacific ones. However, since the brownish colouration of *O. macracantha* provides the main distinction from the very dark *O. septemspinosa*, it seems consistent to treat this specimen from Aldabra as at least subspecifically distinct from the Pacific material.

There is a parallel precedent for this in the reddish-orange subspecies *erythrema* Devaney, 1974, from south-eastern Polynesia, of the confusingly similarly-named *Ophiarachna megacantha* H. L. Clark (from Australia), patterned with grey or brown (though H. L. Clark did not see any live specimens).

Ophiarachna megacantha (with *O. robillardi* de Loriol from Mauritius) and *Ophiarachnella macracantha* (with *O. septemspinosa*) form an interesting convergence. Both pairs of species have a combination of small bare patches of radial and supplementary oral shields, not found elsewhere in *Ophiarachna*, where most species of *Ophiarachnella* have larger bare shields and also have more numerous oral papillae and appressed arm spines. *Ophiarachna megacantha* and *robillardi* are distinguished from *Ophiarachnella macracantha* and *septemspinosa* by the much longer and fewer arm spines, numbering no more than six in the first two and that only at disc diameter 25 mm or more, when the longest lower arm spines are as much as 7 mm long.

The range of *Ophiarachnella macracantha* is extended from the Caroline Islands and Fiji.

Ophiarachnella septemspinosa (Müller & Troschel, 1842)
See: H. L. Clark, 1909 : 126; A. M. Clark & Rowe, 1971 : 126.
Occasionally found under coral rubble along Passe Dubois (060–080), in the lower eulittoral off the research station (054–091), along the sides of Main Channel (108–120). Most common under *Porites* microatolls over sandy gravel in lagoon grass flats (068–083) near West Channels where groups of up to eight individuals were found. D.d. max. = 38 mm; a.l. : d.d. = 4·1 : 1, only a

slight increase in relative arm length with disc size. The largest specimen weighed 29·3 g whereas the largest *Ophiomastix venosa* weighed 23·6 g (d.d. = 41 mm).

Colour in life: uniform dull grey or grey-green overall, radial shields dark brown.

Ophiochaeta hirsuta Lütken, 1869 (with synonym *O. boschmai* A. H. Clark, 1964)
See: A. M. Clark & Rowe, 1971 : 127; Gibbs, Clark & Clark, 1976 : 129.
One specimen under a *Porites* microatoll over sandy gravel in the lagoon grass flats (068–083) near West Channels, two more from coral along Passe Houareau (316–118). D.d. max. = 8·2 mm; a.l. : d.d. = 3·8 : 1.

Colour in life: uniform grey-brown with pale brown banding on the arms, ventrally off-white overall.

The varied occurrence of spinelets on the discs of the four specimens from Aldabra and two from Palau, Caroline Islands, indicate that *Ophiochaeta boschmai* A. H. Clark, 1964 (type locality Molucca Islands) is a synonym of *O. hirsuta* Lütken, 1869. One Aldabra and one Palau specimen have peripheral and ventral spinelets only (intermixed among the indented granules), as thought to be characteristic of *O. boschmai*. The other specimens have spinelets in various degrees of frequency and length also on the upper sides of the discs. The length of the coarser armament on the convex marginal plates of the disc is also variable, being usually almost granuliform but sometimes distinctly elongate.

Cherbonnier & Guille (1978 : 219) have described a new species of *Ophiochaeta*, *O. crinita*, on the basis of a single specimen from Madagascar with the disc armament entirely spiniform except for a few granules near the genital slits.

Ophioconis permixta Koehler, 1905
See: A. M. Clark, 1965 : 63.
Under boulders and coral in the shallow sublittoral off the Settlement (056–100).

Range extended from East Africa and Madagascar.

Ophiopeza fallax Peters, 1851
See: de Loriol, 1893*b*: 4; A. M. Clark & Rowe, 1971 : 127.
One specimen found under a *Porites* microatoll over sandy gravel in lagoon grass flats (068–083) near West Channels. D.d. = 13 mm, a.l. = 43 mm; a.l. : d.d. = 3·3 : 1.

Colour in life: disc covered with smooth grey-brown skin, arms the same colour with red-brown bands up to two segments wide, ventrally off-white overall.

Range extended from East Africa, Madagascar and the Mascarene Islands.

OPHIURIDAE

Ophiolepis cincta Müller & Troschel, 1842 Fig. 22
See: Balinsky, 1957 : 28; Cherbonnier & Guille, 1978 : 232.
Under boulders, particularly buried in sandy gravel in the lower eulittoral of seaward platforms of the west and north coasts, under coral heads and microatolls in the lagoon grass flats (068–083), near West Channels and along Passe Houareau (316–112). D.d. max. 15 mm.

This species occurs in two distinct colour forms. The majority are predominantly dark brown on the disc (sometimes all brown – Fig. 22 right) with some white spots or larger patches, which in three specimens forms a pentaradiate pattern with a more or less regular white patch in each interradius (Fig. 22 top); the upper side of the arms is brown interrupted by white bands in proportion to the extent of white on the disc, the white bands numbering 3–7 per arm. (When dried, the brown usually turns to black or dark grey and the underside is paler, especially the disc. Under the microscope the white areas of the upper side are seen to be finely marbled with dark grey.) In contrast, some specimens had the colour in life uniformly ochre or grey-green on the upper side.

These two colour forms are also correlated with differences in the relative arm length. In life the seven drab uniform specimens collected were estimated (by Sloan) to have a.l. : d.d. = 5·5 : 1, compared with 2·7–3·8 : 1 for 15 of the boldly coloured specimens. (Following some shrinkage of the disc in drying, the ratios have fallen slightly to means of 5·2 : 1 and 3·6 : 1.)

22

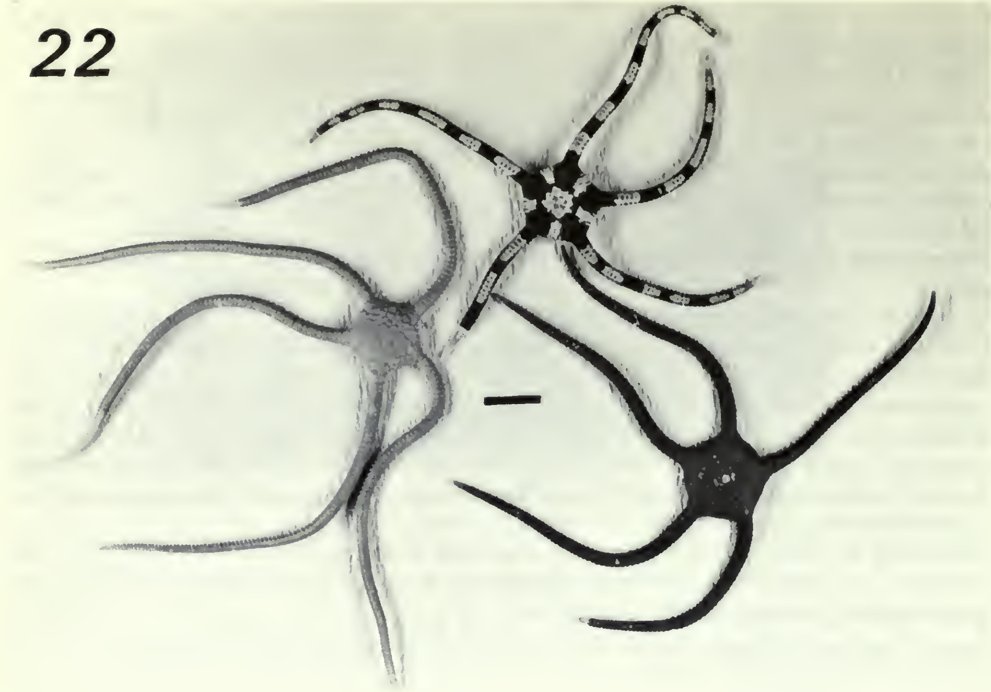


Fig. 22 *Ophiolepis cincta garretti* Lyman (pale specimen on left) and *O. cincta cincta.* (Scale = 10 mm.)

Evidently the patterned form is not restricted to Aldabra since Balinsky (1957) records *O. cincta* at Inhaca, Mozambique, as 'rather brownish with irregular white spots on the disc and white cross-bands on the arms, these white areas being finely marbled with greyish'. Also Cherbonnier & Guille (1978) found specimens from Madagascar (and Dar-es-Salaam, Tanzania) to have the disc 'marron foncé et beige clair . . ., marron foncé dominant' and the arms banded; they give the a.l. as *c.* 3×d.d. In a sample of 38 specimens in spirit in the BMNH collections from Zanzibar the disc colour is now mainly dull dark brown or grey patterned with light grey marbled spots or patches, usually interradially and centrally and sometimes making a regular pentaradiate pattern as in the top specimen in fig. 22. The range of a.l. : d.d. in these specimens is 2·2–4·6 : 1, mean 3·2 : 1 but the sample also includes a single relatively long-armed and uniformly dull brownish coloured specimen with a.l. : d.d. = 4·6 : 1. Three similar drab-coloured specimens from Aldabra collected by Taylor and two from Mauritius have a.l. : d.d. 4·4–5·9 : 1.

The type locality of *O. cincta* is the Red Sea (no details). Müller & Troschel do not describe the disc colour but note that the arms are banded dark and light; a.l. : d.d. they give as only 2·5 : 1. Eleven specimens in the BMNH collections from the Gulf of Aqaba and the southern Red Sea (5–15 years in alcohol) still show broad bands on the arms; their discs are mainly brownish or grey with light grey spots or larger patches, varying in size, shape and position but often with an enlarged central light patch while sometimes the smaller patches are interradial and in one case form a pentaradiate regular pattern. They have a.l. : d.d. 3·1–4·1 : 1, mean 3·7 : 1.

Although all these specimens show the distinctive regular arrangement of small platelets almost encircling the smooth disc plates and bordering each dorsal arm plate on its distal side, thought to be characteristic of *O. cincta*, it is clear that two taxa (best ranked as subspecies in the opinion of A. M. C.) can be distinguished, at least in the western Indian Ocean, one relatively long-armed and drab-coloured and the other shorter-armed and with a bolder and usually patterned colouration. The latter is clearly the nominate subspecies, *O. cincta cincta*, of which the Aldabra specimens may be recognizable as a colour form with a strong tendency for developing a regular pentaradiate pattern.

In seeking a name for the drab-coloured relatively long-armed subspecies, a possible candidate is *Ophiolepis garretti* Lyman, 1865, type locality Kingsmills (i.e. Gilbert) Islands in the Pacific. The holotype and only specimen had a.l. : d.d. 55 : 9 = 6·1 : 1. In life the colour of the disc was uniform brick red but the arms were banded with paler areas. Lyman then thought it distinguishable from *O. cincta* not only by the longer arms but also by the shorter oral shields and the rougher texture of the dorsal arm plates. However, in his *Challenger* report (1882) he synonymized it with *O. cincta*. Unfortunately, no good samples from the Pacific are available. In spite of the banded arms of the holotype of *O. garretti*, the long arms and uniformly coloured disc justify reviving the name for the subspecies showing these characters.

The apparent absence of the widespread species *Ophiolepis superba* H. L. Clark from Aldabra, despite intensive collecting, is notable. This conspicuous ophiuroid with d.d. commonly 15–25 mm has been recorded in the western Indian Ocean from East Africa, Madagascar, Mauritius and from Mahé. It usually has a bold pentaradiate disc pattern of purple (in life) on light brown but in this case the light areas are radial, not interradial.

Ophioplocus imbricatus (Müller & Troschel, 1842)
See: H. L. Clark, 1921 : 143; A. M. Clark & Rowe, 1971 : 128.
Fairly common partially buried in sand or sandy gravel under boulders in the lower eulittoral of the west and north coast seaward platforms, occasionally at the bases of *Thalassodendron* on these platforms as well. D.d. max. = 19·5 mm, arm length very variable in every specimen but a.l. : d.d. usually more than 4 : 1.

Colour in life: darker grey-green overall than *Ophiolepis cincta garretti*, the disc with ill-defined, coarse, dark grey reticulations, arms banded with dark grey, ventrally more grey still with dark grey oral shields.

Class **ECHINOIDEA**

CIDARIDAE

Eucidaris metularia (Lamarck, 1816)
See: Mortensen, 1928 : 386.
Common under boulders and at the bases of sea-grass on the seaward platforms of the west and north coasts, in and under coral in lagoon grass flats near West Channels and Passe Houareau. A ubiquitous species wherever coral and sea-grass occur with the exception of the exposed seaward east and south coasts.

Phyllacanthus imperialis (Lamarck, 1816)
See: Mortensen, 1928 : 504.
Abundant on sponge-covered rocks, along with a large population of *Ophiactis savignyi*, at the tidal intake to the large land-locked marine pool (059–094) on Ile Picard. For a description of this unusual marine pool habitat see Taylor (1971*a* : 196).

Prionocidaris baculosa (Lamarck, 1816)
See: Mortensen, 1928 : 437.
Found under algae and coral amongst *Thalassodendron* on seaward platforms of and in old *Stomopneustes variolaris* burrows at the cliff base of Cinq Cases (396–055).

Prionocidaris verticillata (Lamarck, 1816)
See: Mortensen, 1928 : 428 (as *Plococidaris*).
At the bases of *Thalassodendron* on the west and north coast seaward platforms, under coral heads in lagoon grass flats near West Channels and Passe Houreau. Never as common as *Eucidaris metularia* and rarely found as coral head infauna. Only small specimens were found, e.g. greatest test diameter 20 mm.

DIADEMATIDAE

Astropyga radiata (Leske, 1778)
See: Mortensen, 1940 : 187.
Epifaunal on a sand patch as a group of 20 in the western lagoon (097–105).

Diadema savignyi Michelin, 1845
See: Mortensen, 1940 : 265; A. M. Clark & Rowe, 1971 : 153.
Under boulders in the lower eulittoral of the west and north coast seaward platforms, more common in, but especially under, coral heads in the lagoon grass flats (068–083) near West Channels and in Passe Houareau (316–118). Specimens found were never large, maximum test diameter 50 mm.

Diadema setosum (Leske, 1778)
See: A. M. Clark & Rowe, 1971 : 153; Dart, 1972 : 50 (feeding & ecology); Herring, 1972 : 169 (feeding & ecology).
Reported by Hughes & Gamble (1977), found among sea-grasses on lagoon flats near West Channels (063–089) and by Price (1971), incorrectly identified, from the same area and habitat.

We feel the record needs confirmation as the differences between *D. setosum* and *D. savignyi* are so subtle (see A. M. Clark, 1967 : 49) and *D. setosum* appears to be rare in the Mascarene Islands and East Africa, though it is the dominant or only species in the Red Sea. If correct, it would provide an extension of range.

Echinothrix calamaris (Pallas, 1774)
See: Mortensen, 1940 : 285; Herring, 1972 : 169 (feeding & distribution).
Under boulders in the lower eulittoral of the west and north coast seaward platforms, most common, like *D. savignyi*, in the more sheltered lagoon habitats like the grass flats near West Channels and Passe Houareau where they occur under coral heads and microatolls.

STOMECHINIDAE

Stomopneustes variolaris (Lamarck, 1816)
See: Mortensen, 1935 : 507; Taylor, 1971*a* : 183 (ecology on Aldabra); Herring, 1972 : 169 (feeding & ecology).
Abundant in holes along the lower eulittoral and especially the sublittoral fringe of the exposed east and south coastal platforms. Interestingly, this species was present under rubble on the rock platform at Dune Jean Louis (275–039) whereas the relatively more exposed rock platform near Point Hodoul (407–080) had no rubble present and the animals were found only in holes in intact bedrock.

In the burrows of this species, two species of crustaceans were found: the gnathophyllid shrimp *Gnathophyllum americanum* Guérin, 1856 (normally free-living predators on asteroids and ophiuroids – Dr A. J. Bruce, pers. comm.) and the porcellanid crab *Petrolisthes virgatus* Paulson, 1876 (not reported previously as associated with echinoids and a new locality record for this species – Dr J. Haig, pers. comm.). The crabs at least were found as male/female pairs.

Although unrecorded from the islands of the western Indian Ocean by A. M. Clark & Rowe (1971), this species was in fact collected by J. D. T. at Mahé and reported in Taylor (1968). It is also common in the Mascarene Islands and on the East African coast.

TOXOPNEUSTIDAE

Tripneustes gratilla (Linnaues, 1758)
See: Mortensen, 1943*a* : 500; Herring, 1972 : 169 (feeding & ecology).
Sometimes found under boulders in the lower eulittoral of the west and north coast seaward platforms, but common under microatolls and coral heads on the lagoon grass flats near West Channels and Passe Houareau. As with some other Aldabra echinoids, only small individuals were taken, maximum test diameter 52 mm.

Toxopneustes pileolus (Lamarck, 1816)
See: Mortensen, 1943*a* : 472.
Reported only by Hughes & Gamble (1977) – from a sheltered site in Passe Houareau (319–118).

PARASALENIIDAE

Parasalenia gratiosa A. Agassiz, 1863
See: Mortensen, 1943*b* : 269.
From rubble in the bottom of Passe Dubois, at about 10 m.

Range extended from East Africa and Madagascar.

ECHINOMETRIDAE

Colobocentrotus atratus (Linnaeus, 1758)
See: Mortensen, 1943*b* : 434.
On the lower eulittoral cliff face between Point Hodoul and Anse Cedres (390–103).

Echinometra mathaei (de Blainville, 1825)
See: Mortensen, 1943*b* : 381; Khamala, 1971 : 167 (ecology); Dart, 1972 : 50 (feeding & ecology); Herring, 1972 : 169 (feeding & ecology); Russo, 1977 : 693 (distribution).
The most ubiquitous echinoid on Aldabra, found under boulders, coral heads and in holes on all the seaward shores, in or under coral heads or microatolls in all the channel areas of the lagoon. Most common and reaches its largest size in holes in the lower eulittoral of exposed east and south coast rocky shores, see Taylor (1971*a* : 183) for habitat details.

As with *S. variolaris*, on the south coast *E. mathaei* shares its burrow with the shrimp *G. americanum* or the crab *P. virgatus*.

Echinostrephus molaris (de Blainville, 1825)
See: Mortensen, 1943*b* : 304; Campbell *et al.*, 1973 : 155 (feeding & ecology).
Common in burrows in coral boulders at places where there is plenty of current like any of the channels leading out of the lagoon, also found off the seaward platforms of the west and north coasts, not common in the eulittoral.

Range extended from East Africa, Madagascar and the Mascarene Islands.

Heterocentrotus trigonarius (Lamarck, 1816)
See: Mortensen, 1943*b* : 420.
Spines and test fragments of this species were found among corals at 15 m deep off the research station (052–091), found live in a crevice at the base of cliffs at Point Hodoul (404–105).

ECHINONEIDAE

Echinoneus abnormalis de Loriol, 1883
See: Mortensen, 1948*a* : 80.
In sand under coral heads in the lagoon grass flats (068–083) near West Channels, under coral alongside Passe Dubois (060–080), under boulders in the shallow sublittoral off the research station (052–091).

Range extended from the Mascarene Islands.

Echinoneus cyclostomus Leske, 1778
See: Mortensen, 1948*a* : 75; Rose, 1978 : 199 (ecology).
A shallow burrower in sand under boulders on the seaward platforms of all coasts around Aldabra, also under boulders and coral heads in the lagoon at all the channel areas. Never common.

CLYPEASTERIDAE

Clypeaster fervens Koehler, 1922
See: Mortensen, 1948*b* : 86.
Reported only by Hughes & Gamble (1977) – infauna at sea-grass bases on the seaward platform at Anse Malabar (241–127) on the north coast.

Clypeaster reticulatus (Linnaeus, 1758)
See: Mortensen, 1948*b* : 71.
In sand among sea-grass roots in the lagoon (065–090) near West Channels, on the seaward platform of the west coast, and on sand in the lagoon near Ile Châlen (080–074).

FIBULARIIDAE

Echinocyamus crispus Mazetti, 1896
See: Mortensen 1948*b* : 185.
In sand and coarse gravel along Passe Dubois (060–080) among *Thalassodendron* beds.

Range extended from East Africa and Madagascar.

Fibularia ovulum Lamarck, 1816
See: Mortensen, 1948*b* : 208.
In sand and coarse gravel on the north side of Passe Dubois (060–080) with plentiful *Thalassodendron*. As with the other channel areas, this is a habitat of strong and persistent currents.

Clark & Rowe (1971 : 144) give no record of this species from the islands of the western Indian Ocean but their proposed neotype (p. 168) is in fact from Mahé. This is the first record from Aldabra.

Fibularia volva A. Agassiz, 1846
See: Mortensen, 1948*b* : 213.
Reported only by Hughes & Gamble (1977) – infauna in soft mud at a very sheltered site in the Passe Houareau area (319–119).

If correct, this record extends the range from the Red Sea.

ECHINOLAMPADIDAE

Echinolampas ovata (Leske, 1778)
See: Mortensen, 1948*a* : 275.
Reported only by Hughes & Gamble (1977) – infauna from a muddy, sheltered site in Passe Houareau (319–118).

If correct, this record extends the range from the Mascarene Islands.

SPATANGIDAE

Maretia planulata (Lamarck, 1816)
See: Mortensen, 1951 : 27.
Found in sand in Passe Magnan (063–074) of the West Channels and in sand under boulders at the edge of the seaward platform on the north coast (308–124).

Pseudomaretia alta (A. Agassiz, 1863)
See: Mortensen, 1951 : 58.
Reported only by Price (1971) – from the grass flats on the seaward side of West Channels.

SCHIZASTERIDAE

Schizaster lacunosus (Linnaeus, 1758)
See: Mortensen, 1951 : 300.
Reported only by Hughes & Gamble (1977) – infauna from under a thick stand of *Halimeda* in Passe Houareau (316–119).

Range extended from Natal.

BRISSIDAE

Brissus latecarinatus (Leske, 1778)
See: Mortensen, 1951 : 514.
Infauna associated with sand under sea-grass in Passe Houareau (316–118), in sand under boulders on seaward platforms of the west and north coasts.

Metalia dicrana H. L. Clark, 1917
See: Mortensen, 1951 : 546.
Reported only by Hughes & Gamble (1977) – infauna under sea-grass in the lower eulittoral of the seaward platform at Anse Cèdres (360–112).

Metalia spatagus (Linnaeus, 1758)
See: Mortensen, 1951 : 540.
In sand patches amongst *Thalassodendron* on seaward platforms of the west and north coasts, under boulders at the edges of these platforms, and in sand in all the channels.

Metalia sternalis (Lamarck, 1816)
See: Mortensen, 1951 : 535.
In a sand pocket under boulders on west coast seaward platform (063–128); a large test (126 × 114 mm) was found on the beach at Anse Polymnie (108–124) in the lagoon.

Class **HOLOTHURIOIDEA**

HOLOTHURIIDAE

Some useful colour illustrations to many of the species below are given in the recent paper by Rowe & Doty (1977).

Actinopyga sp. cf. *A. bannwarthi* Panning, 1944
See: Cherbonnier, 1955 : 136.
One specimen only, found on the lagoon grass flats (068–083) near West Channels.

If this specimen is *A. bannwarthi*, it extends the range from the Red Sea.

Actinopyga echinites (Jaeger, 1833)
See: Cherbonnier, 1955 : 136; Rowe & Doty, 1977 : 228.
Reported only by Hughes & Gamble (1977) – from the lower eulittoral among seagrass on the seaward platform at Anse Cèdres (360–112).

Actinopyga mauritiana (Quoy & Gaimard, 1833)
See: Rowe & Doty, 1977 : 228; Bakus, 1968 : 24 (ecology).
An ubiquitous epifaunal species on hard substrates at the edge of the seaward platforms on the west and north coasts and more widespread through the eulittoral on the rock benches of the exposed seaward east and south coasts. Interestingly the *A. mauritiana* on the exposed coasts were much smaller, but more numerous than those on the more sheltered coasts. Occasionally seen on the coral flats in the Main Channel drainage system in the lagoon. The only epifaunal holothuroid on the eulittoral rock benches of the exposed coasts.

Large specimens commonly carried the polychaete *Gastrolipidia davigera* Schmarda, 1861. Some specimens had a parasitic gastropod, *Melanella muelleriae* (Sturany, 1904), projecting from the body wall.

Actinopyga miliaris (Quoy & Gaimard, 1833)
See: Panning, 1944 : 47 (as *A. lecanora miliaris*).
Found on the sand in Passe Dubois (060–080) and on grass flats in the lagoon (083–085).

Bohadschia marmorata Jaeger, 1833
See: Rowe & Doty, 1977 : 229.
Found on lagoon grass flats (068–083) or under the overhang of isolated coral heads near West Channels, usually covered with dead fronds of sea-grass.

Range extended from East Africa and Madagascar.

Labidodemas rugosum (Ludwig, 1875)
See: Théel, 1886 : 226 (as *Holothuria rugosa*).
Common under boulders at the edge of the west coast seaward platform.

Holothuria (*Cystipus*) *rigida* (Selenka, 1867)
See: Rowe & Doty, 1977 : 234.
Not common, found in sand under boulders in the lower eulittoral of the seaward platforms of the west and north coasts, in sand in the lagoon north east Ile Esprit (115–067).

Range extended from East Africa and Madagascar.

Holothuria (*Halodeima*) *atra* Jaeger, 1833
See: Rowe & Doty, 1977 : 230; Bonham & Held, 1963 : 305 (ecology); Bakus, 1968 : 24 (ecology).
Common throughout the whole lagoon but not in the great densities reported in the literature from other sheltered reef and lagoon flats. Occasional on the seaward platforms of the west and north coasts.

Holothuria (*Lessonothuria*) *pardalis* Selenka, 1867
See: Rowe & Doty, 1977 : 233.
Found under boulders over sandy gravel or sand on all the seaward platforms around Aldabra, especially on the more sheltered west and north coast seaward platforms, also in the channel areas of the lagoon under coral heads and microatolls over sandy gravel and sand. It should be noted that the spicules of various specimens which have been attributed to *H. pardalis* show a wide range of form and the species is therefore in need of review (Rowe, pers. comm.).

Holothuria (*Lessonothuria*) *verrucosa* Selenka, 1867
See: Semper, 1968 : 90 (as *Holothuria immobilis*).
One specimen only collected from a sand and coral patch in one of the West Channels.

Holothuria (*Mertensiothuria*) *leucospilota* (Brandt, 1835)
See: Rowe & Doty, 1977 : 233; Bonham & Held, 1963 : 305 (ecology).
Occasionally found under boulders over sand in standing water in the upper eulittoral of the Ile Picard beach-rock (056–100); more common in the lower eulittoral of all the coastal seaward platforms around Aldabra, especially the sheltered west and north coasts; also under coral heads over sand in the channel areas of the lagoon.

Holothuria (*Mertensiothuria*) *pervicax* Selenka, 1867
See: Rowe & Doty, 1977 : 234.
Not too common, usually found under coral over sand in channel areas of the lagoon like Main Channel (104–110), West Channels (068–083) and Passe Houareau (316–118); less commonly seen under coral at the edge of seaward platforms like Dune Jean Louis (275–039).

One specimen had parasitic gastropods, *Melanella muelleriae*, projecting from the body wall.

Holothuria (*Microthele*) *nobilis* (Selenka, 1867)
See: Rowe & Doty, 1977 : 231.
Most individuals were of the black form with the large lateral bumps white; others were uniformly grey. On lagoon grass flats (068–083) and among coral heads near West Channels, near Ile Châlen (080–072). On 23 April 1978 a specimen with one end elevated off the substrate was noted as emitting a milky substance and was probably spawning.

Holothuria (*Platyperona*) *difficilis* Semper, 1868
See: Rowe & Doty, 1977 : 232; Bakus, 1968 : 23 (ecology).
One specimen found under a coral head over sandy gravel on lagoon grass flats (068–083) near West Channels, one specimen found under coral over muddy sand in a mangrove creek at Passe Gionnet (137–120) in the lagoon, one specimen found under boulders over sand on the seaward platform at Anse Var (068–122).

Holothuria (*Selenkothuria*) *moebii* Ludwig, 1883
See: H. L. Clark, 1946 : 426.
One specimen only, found under a boulder in the upper eulittoral of the Ile Picard beach-rock (056–100).

Range extended from the Mascarene Islands.

Holothuria (*Selenkothuria*) *parva* Krauss *in* Lampert, 1885
See: Cherbonnier, 1952 : 503.
Common under boulders over intact bed rock in the upper eulittoral beach-rock of Ile Picard (056–100), also found in sand pockets at the cliff base of Dune d'Messe (265–038) on the exposed south coast. (The identification is by A. M. C.)

Range extended from East Africa and Madagascar.

Holothuria (*Semperothuria*) *cinerascens* (Brandt, 1835)
See: Rowe & Doty, 1977 : 230.
Abundant in crevices and holes in the same lower eulittoral band with the echinoids *Echinometra mathaei* and *Stomopneustes variolaris* on the exposed south and east coasts at Dune Jean Louis (275–039) and near Point Hodoul (407–080); uncommon in the sheltered upper eulittoral beachrock at Ile Picard (056–100) on the more sheltered west coast.

One specimen had several of the parasitic gastropods, *Melanella muelleriae*, on the body wall.

Holothuria (*Theelothuria*) sp. cf. *H. hamata* Pearson, 1913
See: Pearson, 1913 : 51; Cherbonnier, 1955 : 156.
Two specimens taken from amongst algae and sea-grass on the lagoon side of West Channels.

If these specimens are *H. hamata*, the range would be extended to the western Indian Ocean from the Red Sea.

Holothuria (*Theelothuria*) *maculosa* Pearson, 1913
See: Pearson, 1913 : 53 (Aldabra is the type locality for this species).
Recorded only by Hughes & Gamble (1977) – from sea-grass flats in Passe Houareau (316–118).

Holothuria (*Thymiosycia*) *arenicola* Semper, 1868
See: Rowe & Doty, 1977 : 232.
A common, ubiquitous species in sand or sandy gravel under boulders in the lower eulittoral of the seaward platforms on all coasts around Aldabra; also in sand under coral heads and sea-grass in the channel areas of the lagoon.

Some specimens were infested with the parasitic gastropod *Melanella muelleriae* on the body wall.

Holothuria (*Thymiosycia*) *hilla* Lesson, 1830
See: Rowe & Doty, 1977 : 232.
Found under boulders over sandy gravel or coarse rubble in the lower eulittoral of the seaward platforms all around Aldabra, also under coral heads in all the channel areas of the lagoon.

Holothuria (*Thymiosycia*) *impatiens* (Forskaal, 1775)
See: Rowe & Doty, 1977 : 233.
The most common of the ubiquitous cryptic holothurian species, under boulders over sand and sandy gravel on all seaward platforms around Aldabra and, like all the others, more common on the relatively sheltered coastal platforms of the west and north coasts, common under coral heads in the channel areas of the lagoon and occasionally in the coral heads as well.

Holothuria (*Thymiosycia*) *remollescens* Lampert, 1888
See: H. L. Clark, 1946 : 437.
Three specimens were taken from under rubble among sea-grasses on the seaward platform of the west coast.

Range extended from the Red Sea.

STICHOPODIDAE

Stichopus chloronotus Brandt, 1835
See: Rowe & Doty, 1977 : 227; Yamanouchi, 1956 : 347 (feeding & ecology).
The most common epifaunal holothurian species on hard substrates in the sublittoral fringe and shallow sublittoral of the west and north coastal platforms, also a common species on the coral flats and patch reefs in the Main Channel drainage system of the lagoon. Not seen on the exposed rock benches of the east and south coasts.

Humphreys & Lützen (1972) described a new parasitic gastropod, *Megadenus cantharelloides*, from an Aldabra specimen of *S. chloronotus*, living on the inner face of the body wall of *S. chloronotus*.

Stichopus sp. cf. *S. horrens* Selenka, 1867
See: Rowe & Doty, 1977 : 227.

Found under *Porites* microatolls on the lagoon grass flats (068–083) near West Channels and under boulders at the edge of the seaward platform of the west coast.

The length of the larger specimen as preserved is 85 mm, whereas *S. horrens* may exceed 200 mm. This may account for the absence of the large tack-like tables with pointed spires so characteristic of large specimens of *S. horrens* and present in a specimen from Egmont Reef, Chagos Archipelago, recorded under 'Maldive area' by Clark & Rowe (1971). If correct, this new record would extend the range still further. However, Cherbonnier (1967) has recorded a new species, *Stichopus pseudhorrens*, from Eilat, northern Red Sea, the holotype (length 220 mm) also having some tack-like tables. It has some conspicuous conical warts similar to but probably forming more rows than in the Aldabra specimens and also differs in being a dark chestnut colour.

Stichopus sp. cf. *S. variegatus* Semper, 1868
See: James & Pearse, 1969 : 102; Yamanouchi, 1956 : 347 (feeding & ecology).
One specimen of an unusual red colouration found under a *Porites* microatoll on the lagoon grass flats (068–083) near West Channels.

Thelenota ananas (Jaeger, 1833)
See: Rowe & Doty, 1977 : 227.
Found on sand at the bottom of channels between patch reefs in the Main Channel drainage system of the lagoon and on sand off the seaward platform of the north and west coasts at greater than 5 m depth.

Range extended from the Maldive Islands and the Mascarene Islands (unpublished from the BMNH collections) as well as from the West Pacific.

CUCUMARIIDAE

Orbithyone megapodia H. L. Clark, 1938
See: H. L. Clark, 1946 : 396.
Reported only by Hughes & Gamble (1977) from under rubble off the west coast seaward platform.

The species is poorly distinguished, the holotype from northern Australia having spicules only in the tentacles, not the body wall, and measuring only 15 mm in length, so the record is very dubious.

PHYLLOPHORIDAE

Afrocucumis africana (Semper, 1863)
See: Rowe & Doty, 1977 : 226.
Abundant under boulders in the upper eulittoral of the Ile Picard beach-rock (056–100) and common in crevices on the exposed seaward rock benches of the east and south coasts, less common under boulders over gravel on the seaward platforms of the west and north coasts.

SYNAPTIDAE

Euapta godeffroyi (Semper, 1868)
See: Rowe & Doty, 1977 : 235.
Under boulders and at the bases of sea-grass in the lower eulittoral of the sea-grass platforms of the west and north coasts, under coral heads on the grass flats in the lagoon at Passe Houareau and West Channels.

Range extended from the Mascarene Islands.

Polyplectana kefersteini (Selenka, 1867)
See: Rowe & Doty, 1977 : 235.
Some collected in the same areas as *Euapta godeffroyi* above.

Range extended from the Red Sea.

Synapta maculata (Chamisso & Egsenhardt, 1821)
See: Rowe & Doty, 1977 : 234.

Found on *Thalassia* beds on the seaward platform of the west coast and on the seaward side of the West Channels.

CHIRIDOTIDAE

Chiridota stuhlmanni Lampert, 1896
See: Heding, 1931 : 676.
Collected under the upper eulittoral beach-rock of Ile Picard (056–100) and from rubble in Passe Houareau.

Range extended from East Africa.

Chiridota violacea (J. Müller, 1850)
See: Heding, 1928 : 296; Hughes & Gamble, 1977 : 334 (habitats & distribution on Aldabra).
Can be the dominant member of the infauna in certain sheltered, sandy areas in the lagoon (315–117) near Passe Houareau as well as other similar areas.

Range extended from East Africa and Madagascar.

Polycheira rufescens (Brandt, 1835)
See: Heding, 1928 : 306.
Common under boulders on the upper eulittoral beach-rock of Ile Picard (056–100), also one specimen was found under boulders on the lagoon side (063–080) of Passe Dubois.

Acknowledgements

N. A. S. would like to thank the Royal Society for the award of the John Murray Travelling Studentship and for the provision of facilities at its research station on Aldabra, Professors N. B. Marshall and J. D. Pye and Dr A. C. Campbell for their support at Queen Mary College, London, Mr L. U. Mole of the Royal Society for his support and consideration, and especially Ailsa Clark and John Taylor whose encouragement and support made this project possible.

We thank Dr A. J. Bruce (Heron Island Research Station, Queensland) for the shrimp identification; Dr P. E. Gibbs (Marine Biological Station, Plymouth) for the polychaete identification; Dr J. Haig (Allan Hancock Foundation, California) for the crab identification; Professor J. Stock (Zoological Museum, University of Amsterdam) for the pycnogonid identification; Dr A. Waren (Zoological Institute, Göteborg University) for the parasitic mollusc identification; Mr G. L. J. Paterson (BMNH) for valuable assistance with the collection; Dr F. W. E. Rowe (Australian Museum, Sydney) for identification of most of the holothurians. Dr W. F. Humphreys (University of Bath) and Dr R. N. Hughes (University College of North Wales at Bangor) kindly provided unpublished material from their Aldabra fieldwork.

References

Achituv, Y. 1969. Studies on the reproduction and distribution of *Asterina burtoni* Gray and *A. wega* (Asteroidea) in the Red Sea and the Eastern Mediterranean. *Israel J. Zool.* **18** : 329–343.

Bakus, G. J. 1968. Defensive mechanisms and ecology of some tropical holothurians. *Mar. Biol. Berlin* **2** : 23–32.

Balinsky, J. B. 1957. The Ophiuroidea of Inhaca Island. *Ann. Natal Mus.* **14** : 1–33.

Bonham, K. & Held, E. E. 1963. Ecological observations on the sea cucumbers *Holothuria atra* and *H. leucospilota* at Rongelap Atoll, Marshall Islands. *Pacific Sci.* **17** : 305–314.

Campbell, A. C., Dart, J. K. G., Head, S. M. & Ormond, R. F. G. 1973. The feeding activity of *Echinostrephus molaris* (de Blainville) in the central Red Sea. *Mar. Behav. Physiol.* **2** : 155–169.

Chartock, M. A. 1972. The role of detritus in a tropical marine ecosystem: niche separation in congeneric ophiuroids, food partitioning in cryptic invertebrates and herbivore detritus production at Eniwetok, Marshall Islands. Ph.D. thesis, University of Southern California, Los Angeles. 177 pp.

Cherbonnier, G. 1952. Les holothuries de Quoy et Gaimard. *Mém. Inst. r. Sci. nat. Belg.* **44** : 1–50.

—— 1955. Résultats scientifiques des campagnes de la 'Calypso'. Les holothuries de la Mer Rouge. *Annls Inst. océanogr., Monaco* **30** : 129–183.

—— 1967. Deuxième contribution á l'étude des Holothuries de la Mer Rouge collectées par des Israéliens. *Bull. Sea Fish. Res. Stn Haifa* **43** : 55–68, 6 figs.

—— **& Guille, A.** 1978. Echinodermes: Ophiurides. *Faune de Madagascar.* No. 48 : iv + 272 pp.

Clark, A. H. 1941. A Monograph of the Existing Crinoids. I (4a). Superfamily Mariametrida (except the family Colobometridae). *Bull. U.S. natn. Mus.* **82** (4a) : 1–603.

—— 1947. A Monograph of the Existing Crinoids. I (4b). Superfamily Mariametrida (concluded – the family Colobometridae) and Superfamily Tropiometrida (except the families Thalassometridae and Charitometridae). *Bull. U.S. natn. Mus.* **82** (4b): 1–473.

—— 1964. Description of two new species of Ophiuroidea collected during the Snellius Expedition. *Zool. Meded., Leiden* **39** : 385–390.

—— **& Clark, A. M.** 1967. A Monograph of the Existing Crinoids. I (5). Suborders Oligophreata (concluded) and Macrophreata. *Bull. U.S. natn. Mus.* **82** (5) : 1–860.

Clark, A. M. 1965. Japanese and other ophiuroids from the collections of the Münich Museum. *Bull. Br. Mus. nat. Hist.* (Zool.) **13** : 37–71.

—— 1967. Echinoderms from the Red Sea. 2. Crinoids, ophiuroids, echinoids and more asteroids. *Bull. Sea Fish. Res. Stn Israel* **41** : 26–58.

—— 1970. Notes on the family Amphiuridae (Ophiuroidea). *Bull. Br. Mus. nat. Hist.* (Zool.) **19** : 1–81.

—— 1972. Some crinoids from the Indian Ocean. *Bull. Br. Mus. nat. Hist.* (Zool.) **26** : 421–487.

—— 1974. Notes on some echinoderms from southern Africa. *Bull. Br. Mus. nat. Hist.* (Zool.) **26** (6) : 423–487.

—— 1976*a*. Tropical epizoic echinoderms and their distribution. *Micronesica* **12** : 111–117.

—— 1976*b*. Echinoderms of coral reefs. In: O. A. Jones & R. Endean (Editors). *Biology and Geology of Coral Reefs.* 3. Biology **2** : 95–123. New York.

—— **& Rowe, F. W. E.** 1971. *Monograph of the Shallow-Water Indo-West Pacific Echinoderms.* 1–238 pp., 31 pls. London.

Clark, H. L. 1909. Notes on some Australian and Indo-Pacific echinoderms. *Bull. Mus. comp. Zool. Harv.* **52** : 107–135.

—— 1921. The Echinoderm fauna of Torres Strait. *Pap. Dep. mar. biol. Carnegie Instn Wash.* **10** : 1–233.

—— 1939. Ophiuroidea. *Scient. Rep. John Murray Exped.* **6** : 29–136.

—— 1946. The Echinoderm fauna of Australia. *Publs Carnegie Instn* No. 566 : 1–567.

Dart, J. K. G. 1972. Echinoids, algal lawn and coral recolonization. *Nature* **239** : 50–51.

Devaney, D. M. 1967. An ectocommensal polychaete associated with Indo-Pacific echinoderms, primarily ophiuroids. *Occ. Pap. Bernice P. Bishop Mus.* **23** : 287–304.

—— 1970. Studies on Ophiocomid brittlestars. I. A new genus (*Clarkcoma*) of Ophiocominae with a re-evaluation of the genus *Ophicoma. Smithson. contr. Zool.* No. 51 : 1–41.

—— 1974. Shallow-water asterozoans of southeastern Polynesia. 2. Ophiuroidea. *Micronesica* **10** : 105–204.

—— 1977. *Ophiomastix koehleri*, a new ophiocomid brittlestar (Echinodermata : Ophiuroidea) from the western Indian Ocean. *Proc. biol. Soc. Wash.* **90** : 274–283.

Fishelson, L. 1971. Ecology and distribution of the benthic fauna in the shallow waters of the Red Sea. *Mar. Biol. Berlin* **10** : 113–133.

Fisher, W. K. 1919. Starfishes of the Philippine seas and adjacent waters. *Bull. U.S. natn. Mus.* **100** : 1–711.

Gibbs, P. E. 1969. Aspects of polychaete ecology with particular reference to commensalism. *Phil. Trans. R. Soc.* ser. B **255** : 443–458.

—— 1971. The polychaete fauna of the Solomon Islands. *Bull. Br. Mus. nat. Hist.* (Zool.) **21** : 99–211.

—— **Clark, A. M. & Clark, C. M.** 1976. Echinoderms from the northern region of the Great Barrier Reef. *Bull. Br. Mus. nat. Hist.* (Zool.) **30** : 103–144.

Heding, S. G. 1928. Synaptidae. *Vidensk. Meddr dansk naturh. Foren.* **85** : 105–323.

—— 1931. Über die Synaptiden des Zoologischen Museums zu Hamburg. *Zool. Jb.* (*Syst.*) **61** : 637–696.

Herring, P. J. 1972. Observations on the distribution and feeding habits of some littoral echinoids from Zanzibar. *J. nat. Hist.* **6** : 169–175.

Hughes, R. N. 1977. The biota of reef flats and limestone cliffs near Jeddah, Saudi Arabia. *J. nat. Hist.* **11** : 77–96.

—— **& Gamble, J. C.** 1977. A quantitative survey of the biota of intertidal soft substrata on Aldabra Atoll, Indian Ocean. *Phil. Trans. R. Soc.* Ser. B. **279** : 327–355.

Humphreys, W. F. & Lützen, J. 1972. Studies on parasitic gastropods from echinoderms. I. On the structure and the biology of the parasitic gastropod *Megadenus canthrelloides* n. sp., with comparisons on *Paramegadenus* n.g. *Biol. Skr.* **19** : 1–27.

James, D. B. & Pearse, J. S. 1969. Echinoderms from the Gulf of Suez and the Northern Red Sea. *J. Mar. Biol. Ass. India* **11** : 78–125.

Jangoux, M. 1973*a*. Les asteries de l'Ile d'Inhaca (Mozambique) (Echinodermata : Asteroidea). 1. Les espèces recoltées et leur repartition geographique. *Annls Mus. r. Afr. cent.* (Ser. 8 Sci. zool.) No. 208 : 1–50.

—— 1973*b*. Le genus *Neoferdina* Livingstone (Echinodermata, Asteroidea : Ophidiasteridae). *Rev. Zool. Bot. afr.* **87** : 775–794.

Khamala, C. P. M. 1971. Ecology of *Echinometra mathaei* (Echinoidea : Echinodermata) at Diani Beach, Kenya. *Mar. Biol. Berlin* **11** : 167–172.

Kissling, D. L. & Taylor, G. T. 1977. Habitat factors for reef-dwelling ophiuroids in the Florida keys. In: Taylor, D. L. (Editor). *Proceedings of the Third International Coral Reef Symposium.* University of Miami. pp. 225–231.

Kohn, A. J. 1971. Diversity, utilization of resources, and adaptive radiation in the shallow-water marine invertebrates of tropical ocean islands. *Limnol. Oceanogr.* **16** : 332–348.

Laxton, J. H. 1974. A preliminary study of the biology and ecology of the blue starfish *Linckia laevigata* (L.) on the Australian Great Barrier Reef and an interpretation of its role in the coral reef ecosystem. *Biol. J. Linn. Soc.* **6** : 47–64.

Loriol, P. de. 1885. Catalogue raisonné des Echinodermes recueillis par M. V. de Robillard a l'Ile Maurice 2. Stellerides. *Mem. Soc. Phys. Hist. nat. Genève* **29** : 1–84.

—— 1893*a*. Echinodermes de la Baie d'Amboine. *Revue suisse Zool.* **1** : 359–426.

—— 1893*b*. Catalogue raisonné des Echinodermes recueillis par M. V. de Robillard a l'Ile Maurice. 3. Ophiurides et Astrophytides. *Mem. Soc. Phys. Hist. nat. Genève* **32** : 1–63.

Lyman, T. 1865. Ophiuridae and Astrophytidae. *Illust. Cat. Mus. comp. Zool. Harv.* No. 1 : 1–200.

—— 1882. Ophiuroidea. *Rep. scient. Results Voy. Challenger.* Zool. **5** : 1–386.

Magnus, D. B. E. 1967. Ecological and ethological studies and experiments on the echinoderms of the Red Sea. *Stud. Trop. Oceanogr.* **5** : 635–664.

Marsh, L. M. 1977. Coral reef asteroids of Palau, Caroline Islands. *Micronesica* **13** : 251–281.

Mortensen, T. 1928. *Monograph of the Echinoidea.* **1.** Cidaroidea. 1–551. Copenhagen.

—— 1933. Biological observations on ophiurids, with descriptions of two new genera and four species. *Vidensk. Meddr dansk naturh. Foren.* **93** : 171–194.

—— 1935. *Monograph of the Echinoidea.* **2.** Bothriocidaroida, Melonechinoida, Lepidocentroida, and Stirodonta. 1–647. Copenhagen.

—— 1940. *Monograph of the Echinoidea.* **3** (1). Aulodonta. 1–370. Copenhagen.

—— 1943*a*. *Monograph of the Echinoidea.* **3** (2). Camarodonta 1. 1–533. Copenhagen.

—— 1943*b*. *Monograph of the Echinoidea.* **3** (3). Camarodonta 2. 1–446. Copenhagen.

—— 1948*a*. *Monograph of the Echinoidea.* **4** (1). Holectypoida and Cassiduloida. 1–371. Copenhagen.

—— 1948*b*. *Monograph of the Echinoidea.* **4** (2). Clypeastroida. 1–471. Copenhagen.

—— 1951. *Monograph of the Echinoidea.* **5** (2). Spatangoida 2. 1–593. Copenhagen.

Panning, A. 1944. Die Trepangfischerei. *Mitt. zool. StInst. Hamb.* **49** : 1–76.

Pearson, J. 1913. Notes on the Holothuroidea of the Indian Ocean. *Spolia zeylan.* **9** : 173–190.

Price, J. H. 1971. The shallow sublittoral marine ecology of Aldabra. *Phil. Trans. R. Soc.* Ser. B **260** : 123–171.

Rideout, R. S. 1978. Asexual reproduction as a means of population maintenance in the coral reef asteroid *Linckia multifora* on Guam. *Mar. Biol. Berlin* **47** : 287–295.

Rose, E. P. F. 1978 [1976]. Some observations on the recent holectypoid echinoid *Echinoneus cyclostomus* and their palaeoecological significance. *Thalassia jugosl.* **12** : 299–306.

Rowe, F. W. E. & Doty, J. E. 1977. The shallow-water holothurians of Guam. *Micronesica.* **13** : 217–250.

Russo, A. R. 1977. Water flow and the distribution and abundance of echinoids (genus *Echinometra*) on an Hawaiian reef. *Aust. J. Mar. Freshwater Res.* **28** : 693–702.

Sale, P. F., Potts, D. C. & Frankel, E. 1976. Recent studies on *Acanthaster planci. Search* **7** : 334–338.

Semper, C. 1868. Holothurien. *Reisen in Archipel der Philippinen.* 2. Wissenschaftliche Resultate. 1–288. Weisbaden.

Sloan, N. A. 1979. A pycnogonid-ophiuroid association. *Mar. Biol. Berlin* **52** : 171–176.

—— (in press). Microhabitat and resource utilization in cryptic rocky intertidal echinoderms at Aldabra Atoll, Seychelles. *Mar. Biol. Berlin*

Stock, J. 1979. *Anoplodactylus ophiurophilus* n. sp., a sea spider associated with brittle stars in the Seychelles. *Bijdr. Dierk.* **48** : 156–160.

Takeda, M., Miki, M., Asai, M. & Suzuki, K. 1976. *Halicarcinus orientalis* Sakai (Crustacea : Hymenosomatidae) associated with *Ophiocoma brevipes* Peters (Ophiuroidea : Ophiocomidae) from Hochijo Island. *Bull. natn. Sci. Mus. Tokyo* (Zool.) **2** : 33–38.

Taylor, J. D. 1968. Coral reefs and associated invertebrate communities (mainly molluscan) around Mahé, Seychelles. *Phil. Trans. R. Soc.* Ser. B **254** : 129–206.

—— 1971*a*. Intertidal zonation at Aldabra Atoll. *Phil. Trans. R. Soc.* Ser. B. **260** : 173–213.

—— 1971*b*. Observations on the shallow-water marine fauna of Diego Garcia. *Atoll. Res. Bull.* No. 149 : 31–39.

—— 1976. Habitats, abundance and diets of Muricacean gastropods at Aldabra Atoll. *J. Linn. Soc.* (Zool.) **59** : 165–193.

Taylor, J. D. & Lewis, M. S. 1970. The flora, fauna and sediments of the marine grass beds of Mahé, Seychelles. *J. nat. Hist.* **4** : 199–220.

Théel, H. 1886. Holothurioidea. Part 2. *Rep. scient. Results Voy. Challenger*. Zool. **39** : 1–290.

Thomassin, B. A. 1976. Feeding behaviour of the felt-, sponge- and coral-feeder sea stars, mainly *Culcita schmideliana*. *Helgoländer wiss. Meeresunters.* **28** : 51–65.

Trudgill, S. T. 1976. The marine erosion of limestones on Aldabra Atoll, Indian Ocean. *Z. Geomorph.* n. f. **26** : 164–200.

Westoll, T. S. & Stoddart, D. R. 1971. (Editors). A discussion on the results of the Royal Society expedition to Aldabra 1967–1968. *Phil. Trans. R. Soc.* Ser. B **260** : 1–654.

Yamaguchi, M. 1977*a*. Population structure, spawning, and growth of the coral reef asteroid *Linckia laevigata* (Linnaeus). *Pacific Sci.* **31** : 13–30.

—— 1977*b*. Larval behaviour and geographic distribution of coral reef asteroids in the Indo-West Pacific. *Micronesica* **13** : 283–296.

Yamanouchi, T. 1956. The daily activity rhythms of the holothurians in the coral reefs of Palao Islands. *Publs Seto mar. Biol. Lab.* **5** : 347–362.

Manuscript accepted for publication 23 March 1979

British Museum (Natural History) also publishes the following works on **Echinoderms**

Catalogue of the recent sea-urchins (Echinoidea) in the collection of the British Museum (Natural History). H. Lyman-Clarke
1925, xxviii + 250 pp, 12 plates, systematic and alphabetical indexes and list of types, £8·25

Monograph of the shallow-water Indo-West Pacific Echinoderms. A. M. Clark and F. W. E. Rowe
1971, ix + 238 pp, 31 plates, coloured frontispiece, 100 text figures, 4to, £19·00

The Echinoderms of Southern Africa. A. M. Clark
1976, 276 pp, 276 diagrams, 4to boards, £20·00

Starfishes and related Echinoderms. A. M. Clark.
1968; 3rd ed. 1977, 160 pp, text figures, many colour plates, paper-back £3·00
Joint with T. F. H. Publications Inc. Ltd.

Lists of all BM(NH) publications are available free on request to:

Publications Sales
British Museum (Natural History)
Cromwell Road
London SW7 5BD

Titles to be published in Volume 37

Miscellanea

The echinoderms of Aldabra and their habitats. By N. A. Sloan, Ailsa M. Clark & J. D. Taylor

The Fellodistomidae (Digenea) of fishes from the northeast Atlantic. By Rodney A. Bray & David L. Gibson

The anatomy, phylogeny and classification of bariliine cyprinid fishes. By G. J. Howes

Printed by Henry Ling Ltd, Dorchester

Bulletin of the
British Museum (Natural History)

The anatomy, phylogeny and classification of bariliine cyprinid fishes

G. J. Howes

Zoology series Vol 37 No 3 31 January 1980

The *Bulletin of the British Museum* (*Natural History*), instituted in 1949, is issued in four scientific series, Botany, Entomology, Geology (incorporating Mineralogy) and Zoology, and an Historical series.

Papers in the *Bulletin* are primarily the results of research carried out on the unique and ever-growing collections of the Museum, both by the scientific staff of the Museum and by specialists from elsewhere who make use of the Museum's resources. Many of the papers are works of reference that will remain indispensable for years to come.

Parts are published at irregular intervals as they become ready, each is complete in itself, available separately, and individually priced. Volumes contain about 300 pages and are not necessarily completed within one calendar year. Subscriptions may be placed for one or more series. Subscriptions vary according to the contents of the Volume and are based on a forecast list of titles. As each Volume nears completion, subscribers are informed of the cost of the next Volume and invited to renew their subscriptions. Orders and enquiries should be sent to:

Publications Sales,
British Museum (Natural History),
Cromwell Road,
London SW7 5BD,
England

World List abbreviation: *Bull. Br. Mus. nat. Hist.* (Zool.)

© Trustees of the British Museum (Natural History), 1980

ISSN 0007–1498

Zoology series
Vol 37 No 3 pp 129–198

British Museum (Natural History)
Cromwell Road
London SW7 5BD

Issued 31 January 1980

GENERAL
- 4 FEB 19
LIBRARY
NATURAL HIST

The anatomy, phylogeny and classification of bariliine cyprinid fishes

G. J. Howes
Department of Zoology, British Museum (Natural History), Cromwell Road, London SW7 5BD

Contents

Synopsis 129
Introduction 129
Specimens examined 130
Abbreviations used in the figures 130
Anatomical description of *Opsariichthys*, *Zacco*, *Luciosoma*, *Barilius* and *Engraulicypris* 131
  Osteology 131
  External anatomical characters 171
  The brain 177
  Summary of characters 179
Relationships of the bariliine genera 179
  Classification of *Barilius* 180
  Classification of *Leptocypris* 181
  Classification of *Engraulicypris* 182
  Classification of *Rasbora* (in part) 182
  Parluciosoma gen. nov. 183
  Megarasbora Günther, 1868 183
Interrelationships and classification of the bariliine genera 183
Interrelationships of the bariliine group 184
Biogeography of the bariliines 186
Conclusions 187
Acknowledgements 188
Appendix 1. Annotated list of bariliine genera and species 188
Appendix 2. A note on the taxa formerly included in *Engraulicypris* . . . 195
References 196

Synopsis

The osteology, external anatomical features and gross brain morphology of the cyprinid fish genera *Opsariichthys*, *Zacco*, *Luciosoma*, *Barilius* and *Engraulicypris* are described and compared. With the exception of *Zacco* a series of synapomorph characters are identified in these genera which enable them to be related as a monophyletic assemblage termed the *bariliine group*. The distribution of certain characters demands a reclassification of the considered genera. Species formerly included in *Barilius* are now referred to four genera, *Barilius*, *Opsaridium*, *Raiamas* and *Leptocypris*. *Engraulicypris* is recognized as monotypic and forming the sister group to *Leptocypris*. The identification of synapomorphies in *Luciosoma* and some species of *Rasbora* requires the establishment of a new genus, *Parluciosoma*, to contain the latter. *Megarasbora* is identified as a member of the bariliine group and as representing a plesiomorph luciosomine. The geographic distribution of the group is summarized. Relationships of the bariliines with other monophyletic groups is unresolved, but the chelines are nominated as the likely sister group. *Zacco* does not share any of the derived characters that relate the bariliine genera and it is suggested that its closest relatives are to be found amongst the alburnine cyprinids. Appendices are included which contain annotated lists of the bariliine taxa and notes on the generic allocation of those species previously included in *Engraulicypris*.

Introduction

C. Tate Regan (1911) was the first author to consider *Opsariichthys* as a primitive or generalized cyprinid. He did so on the basis of its possessing triserial pharyngeal teeth, a 'complete series' of

Bull. Br. Mus. nat. Hist. (Zool.) **37** (3): 129–198 Issued 31 January 1980

circumorbitals, large posttemporal fossae, second and third vertebrae separated, a fenestra between the quadrate and the metapterygoid and on the form of the cleithrum.

Regan's opinion of the primitive nature of *Opsariichthys* has been accepted by all subsequent authors who have had cause to comment on cyprinid phylogeny (see, for example, Ramaswami, 1955; Weitzman, 1962; Greenwood *et al.*, 1966; Roberts, 1973). The characters enumerated by Regan do, indeed, appear to be plesiomorph for the Cyprinidae and as such are of little value in indicating the relationships of *Opsariichthys*.

In an earlier paper (Howes, 1978) I described and commented upon some anatomical features of *Opsariichthys* and compared them with similar characters in other cyprinid genera. It is now possible to present a more detailed description of osteological and other anatomical features of *Opsariichthys* and to evaluate them in terms of their plesiomorphy and apomorphy. From my earlier studies (Howes, 1978) I formed the opinion that *Opsariichthys* was related to *Barilius* and, furthermore, that *Luciosoma* also shared characters linking it with these taxa. (It must be pointed out here that my earlier remarks concerning *Barilius* (Howes, 1978) mostly refer to *B. bola* and *B. microcephalus*, taxa which this present study shows to be derived members of the genus.) As this study progressed it became evident that *Engraulicypris sardella* was also allied to *Barilius* but that it had no relationship with other species assigned to *Engraulicypris*. Thus an anatomical description of this taxon is also included.

Previous authors had regarded *Zacco* as the closest relative of *Opsariichthys*. Contrary to their opinion, the studies reported herein show that *Zacco* does not belong to the same monophyletic assemblage as *Opsariichthys*; in order to show why this is so, the anatomy of *Zacco* is described along with that of the other genera.

The data are presented in the form of character headings under which appear descriptions for each genus studied, followed by a comparative analysis at the end of each section.

An annotated list of the taxa comprising the bariliine group is given in Appendix 1 (p. 195), and a list of those taxa formerly included in *Engraulicypris* in Appendix 2 (p. 196).

Specimens examined

Skeletal and alizarin material of representatives of all bariliine genera has been examined. Dissections have been made on a total of *c.* 50 species and all specimens have been radiographed. All the type specimens of species currently assigned to *Engraulicypris* and *Chelaethiops* have been examined. A complete list of specimens used in this study is deposited in the Fish Section of the British Museum (Natural History).

Abbreviations used in the figures

A1	Outer division of *adductor mandibulae* muscle	EPO	Epioccipital
AA	Anguloarticular	ES	Extrascapular
AHF	Anterior hyomandibular fossa	EXO	Exoccipital
AL	Axial lobe of pectoral fin	F	Frontal
AP	Apophysial platform	FC	Foramen for carotid artery
AS	Axial scale	FF	Frontal fossa
BO	Basioccipital	FG	Frontal groove
BOP	Basioccipital plate	FO	Optic foramen
CE	Cerebellum	FR	Frontal ring
CL	Cleithrum	FIII	Foramen for oculomotor nerve
CLA	Claustrum	FIV	Foramen for trochlear nerve
COR	Coracoid	FIX	Foramen for 9th cranial nerve
CU	Cavum utriculus	HMF	Hyomandibular fossae
EB	Epibranchial	HY	Hypural (numbered)
EM	Exit of the posterior myodome	HYP	Hypurapophysis
EP	Epural	IC	Intercalar
		IF	Infrapharngobranchials (numbered)

INC	Incus
IO	Infraorbitals (numbered)
KE	Kinethmoid
LC	Lateral commissure
LE	Lateral ethmoid
LJB	Lateral jugular bridge
LKE	Ligament connecting kinethmoid to mesethmoid (divided)
LKM	Ligament connecting kinethmoid to maxilla
LKP	Ligament connecting kinethmoid to premaxillary ascending process
LP1	Lateral process of 1st vertebra
LP2	Lateral process of 2nd vertebra
LPE	Ligament connecting palatine with ethmoid
LPEK	Ligament connecting palatine with ethmoid and kinethmoid
LPM	Ligament connecting palatine with maxilla
LTF	Lateral temporal fossa
LOC	Lateral occipital fenestra
MC	Mesocoracoid
ME	Mesethmoid
MEC	Mesencephalon
MMP	Maxillary medial process
MX	Maxilla
MYO	Posterior myodome
MYR	Posterior myodome roof
N	Nasal
NC	Neural complex
NP2	Neural plate of 2nd vertebra
NP3	Neural plate of 3rd vertebra
NS4	4th neural spine
OL	Olfactory lobe
OS	Orbitosphenoid
OSE	Orbitosphenoid septum
OSS	Os suspensorium
OT	Olfactory tract
PA	Parietal
PAP	Parasphenoid ascending process
PC	Postcleithrum
PE	Preethmoid
PH	Parhypural
PHF	Posterior hyomandibular fossa
PLP	Vomerine process for attachment of palatine ligament
PMX	Premaxilla
PPJ	Posterior opening of pars jugularis
PRO	Prootic
PS	Parasphenoid
PSFF	Foramen connecting posttemporal and subtemporal fossae
PTE	Pterotic
PTEP	Pterotic process
PTF	Posttemporal fossa
PTS	Pterosphenoid
PTT	Posttemporal
PU1+UI	Fused preural and ural centra
RA	Retroarticular
RAD	Radial
SC	Supracleithrum
SCA	Scaphium
SCP	Scapula
SE	Supraethmoid
SO	Supraoccipital
SOR	Supraorbital
SP	Sphenotic
STF	Subtemporal fossa
TEL	Telencephalon
TR	Tripus
UN	Uroneural
V	Vertebra
VF	Vomerine foramen
VO	Vomer

Note on the figures

All anatomical drawings captioned *Opsariichthys* are of specimens of *Opsariichthys uncirostris bidens*. Unless otherwise stated the scale on all figures indicates 3 mm.

Anatomical description of *Opsariichthys, Zacco, Luciosoma, Barilius and Engraulicypris*

Osteology

Ethmo-vomerine region

Opsariichthys

The *supraethmoid* (SE, Figs 1–3) is a wide bone with a flat dorsal surface and an irregular posterior border sutured to the frontals. The lateral margin of the supraethmoid is gently concave and along this concavity lies the nasal. The supraethmoid's anterior border is thickened and bears a concave notch.

The *mesethmoid* (ME, Figs 1–3) underlies the supraethmoid and is composed of two lateral walls fused anteriorly bearing a sloped concavity (a continuation of the supraethmoid notch) which accommodates the kinethmoid. Antero-ventrally the mesethmoid is produced into a wedge-shaped surface that provides part of the preethmoid fossa. The posterior border of the mesethmoid wall is deeply notched so as to form part of the olfactory foramen.

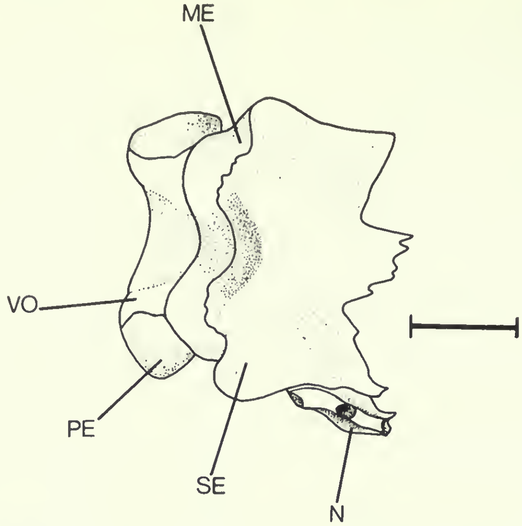


Fig. 1 *Opsariichthys.* Dorsal view of ethmoid region.

Each *preethmoid* (PE, Figs 1–3) is a large irregular hemispherical bone which lies in the fossa formed from the mesethmoid and vomer. The preethmoid does not lie flush with the edges of these two bones but leaves a wide margin of each exposed. In a dissection it is found that the cartilage which covers the preethmoid fills this surrounding area. In a specimen of 38·5 mm SL the preethmoids are small, partially ossified elements occupying only the vomerine part of the fossa.

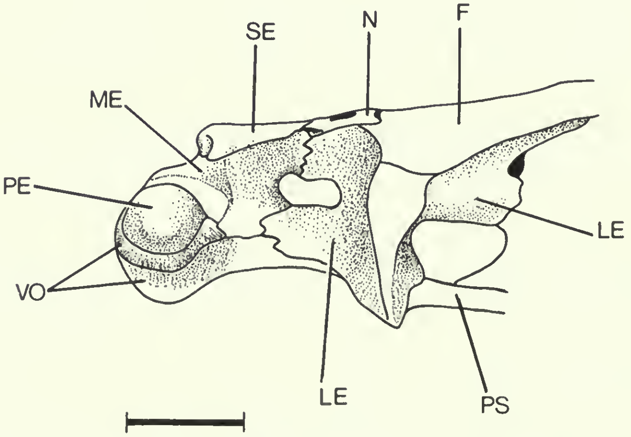


Fig. 2 *Opsariichthys.* Lateral view of ethmo-vomerine region.

Each *lateral ethmoid* (LE, Figs 2 & 3) contacts the dorsal and ventral parts of the mesethmoid, the space between the bones forming part of the olfactory foramen. Laterally, the bone is produced as a thick wall with a wide triangular base. The dorsal surface of the wall is covered by the frontal. The orbital face of the lateral ethmoid is concave and its posterior margin bears a notch through which passes the superficial ophthalmic nerve. The posterior margin of the orbital part of the bone is sutured to the orbitosphenoid, and the dorsal part to the frontal. Medially, the lateral ethmoids meet above the parasphenoid. There is no anterior myodome.

The *kinethmoid* when viewed laterally is seen as an elongated S (Fig. 4A). The dorsal curvature expands into two heads upon which are attached the ligaments joining the bone to the premaxillaries. A ledge along the lateral face of the bone also supports a ligament. This ligament runs from the maxilla and becomes bipartite, one part inserting on the dorsal surface of the ledge, the other, on its ventral surface (Fig. 4B). Basally the kinethmoid is strongly curved towards the ethmo-vomerine complex and it is this part of the bone which is seated in the anterior groove of the vomer. Connection with the ethmo-vomerine block is *via* a bipartite ligament which inserts on a tissue sheath that encloses the ventral half of the kinethmoid (Fig. 4C).

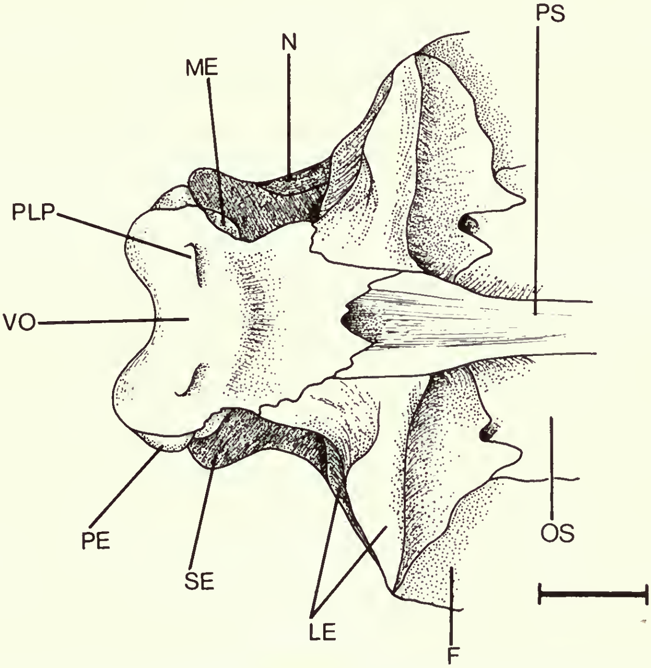


Fig. 3 *Opsariichthys.* Ventral view of ethmo-vomerine region.

The vomer (V, Figs 1–3) is short, its posterior margin extending to a line of the lateral ethmoid walls. Anteriorly it curves ventrad and is transversely convex. The anterior border is concave and bears a wide groove to accommodate the kinethmoid. The ventral surface of the vomer bears, on either side of the midline, two small processes (PLP) onto which the palatine ligament attaches. Laterally the bone forms into a wedge-shaped platform which provides the lower part of the preethmoid fossa. The vomer is overlain anteriorly by the ethmoid and posteriorly by the parasphenoid. There is a cavity between the posterior part of the vomer and the parasphenoid into which insert the ligaments attaching the dorsal borders of the suspensorial elements to the length of the parasphenoid. Postero-laterally the vomer is sutured to the bases of the lateral ethmoids.

Zacco

Zacco differs from *Opsariichthys* in that the *mesethmoid* is narrower and deeper with a ventrolateral nasal cavity; the dorsal surface of the *supraethmoid* is strongly curved rostrad; the olfactory foramen scarcely indents the posterior border of the mesethmoid. The depth and curvature of the ethmoid block is particularly noticeable in *Zacco platypus* (Fig. 5). The *lateral ethmoids*

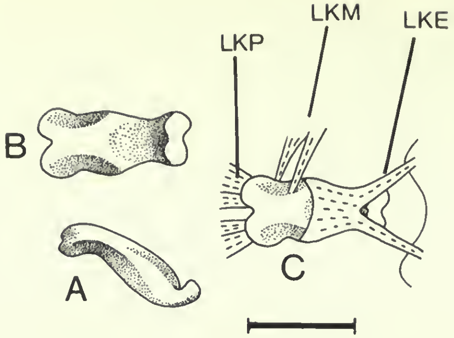


Fig. 4 *Opsariichthys*. Kinethmoid in A, lateral, and B, ventral view. C. Ligamentous connections, ventral view.

are thicker basally and laterally truncated; medially they are indented to form a shallow anterior myodome. The *vomer* is thinner than that of *Opsariichthys*, contributes less to the preethmoid fossa, extends further forward and bears a deeper anterior notch. The *preethmoids* are smaller; the *kinethmoid* is longer and more tubular with a gutter-like groove along its anterior face, its dorsal surface is expanded into two rounded heads which curve forward and are attached to the premaxillaries by ligaments (Fig. 8A).

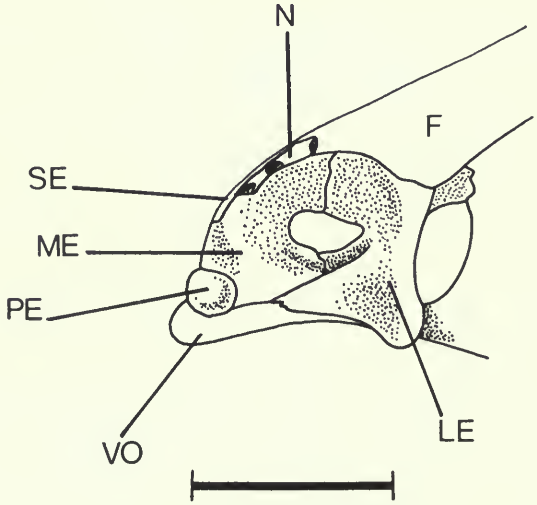


Fig. 5 *Zacco platypus*. Lateral view of ethmo-vomerine region.

Luciosoma

Luciosoma differs from *Opsariichthys* in the following features: the *supraethmoid* is more extensive its dorsal surface having a bowl-shaped depression for accommodating the kinethmoid (Fig. 6); the kinethmoid is S-shaped but more compressed; the *preethmoids* are exposed ventrally, not being completely covered by the vomer; the walls of the *lateral ethmoids* are curved anteriorly and thickened basally, they contain the major part of the olfactory nerve foramen which is produced anteriorly as a bony tube. The orbital part of each lateral ethmoid is inflated. The *vomer* is deeply concave and not swollen as in *Opsariichthys*.

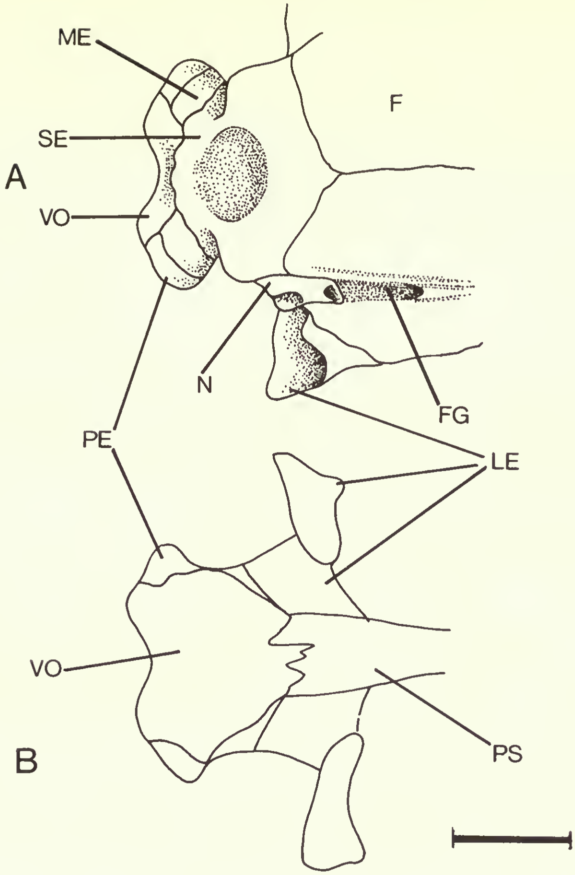


Fig. 6 *Luciosoma bleekeri*. Ethmo-vomerine region in A, dorsal and B, ventral views.

Barilius

Barilius displays considerable variation in the morphology of the ethmo-vomerine region and, as in this and other characters to be discussed, at least three major groups of species can be distinguished. For the purposes of the descriptive anatomical section these are designated as *Groups A*, *B* and *C*. Formal taxonomic treatment of these groups is given in pp. 189–193. Differences are as follows:

Group A. The *mesethmoid* narrow and deep; dorsal surface of *supraethmoid* strongly curved rostrad; *kinethmoid* rod-like with a groove along the anterior surface; *lateral ethmoids* laterally truncated, not extending beyond the frontal margin; *preethmoids* reduced; *vomer* short and deeply notched anteriorly.

Examples of this group of species are *Barilius barila* and *B. ornatus* (see p. 189).

Group B (Fig. 7). The *mesethmoid* is wide and shallow, the dorsal surface of the *supraethmoid* is flat or gently sloped rostrad; the *kinethmoid* bears greatly expanded dorsal heads which give the bone a triangular appearance (Fig. 8B). These heads articulate closely with the premaxillaries, connection being effected through a broad, ligamentous sheet. Whereas in the two Asian species assigned to this group the ventral aspect of the kinethmoid is curved backwards as in *Opsariichthys* in the Africa species it is rounded or curved forward. The *vomer* is short but widely flared anteriorly, medially it is deep and rises steeply beneath the ethmoid.

Examples of species in this group are *Barilius bola*, *B. loati* and *B. salmolucius* (see p. 193).

Group C. The *mesethmoid* is wide and deep, the dorsal surface of the *supraethmoid* slopes rostrad; the *kinethmoid* is rod-like and the *vomer* greatly thickened anteriorly.

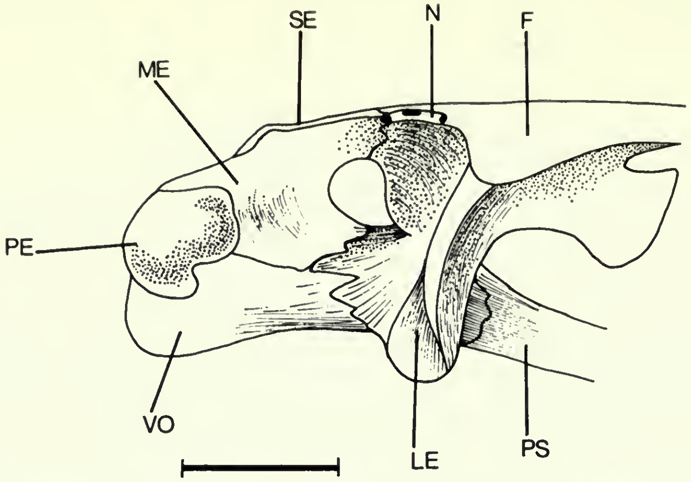


Fig. 7 *Barilius bola*. Lateral view of ethmo-vomerine region.

Examples of species in this group are *Barilius microcephalus*, *B. zambesensis* and *B. ubangensis* (see p. 191).

Engraulicypris

Engraulicypris differs markedly from the genera described above. The ethmoid block (*supraethmoid+mesethmoid*) is elongate and shallow (Figs 9A–E), its anterior border deeply indented in the shape of a horseshoe. Each arm is broadly bevelled ventro-laterally so as to accommodate the underlying vomer. The anterior face of each arm is broad and sloped backwards at 45° to the vertical, on its medial tip there is a prolongation. The *supraethmoid* has a slightly convex lateral margin and a shallow medial depression, its posterior border forming an irregular suture with the frontals. Each large *preethmoid* (Fig. 9C) lies antero-laterally to its respective ethmoid arm, ventrally it is supported by the vomer. Each *lateral ethmoid* (Fig. 9E) scarcely extends from below its respective frontal. The olfactory foramen is contained almost entirely within the bone's medial face.

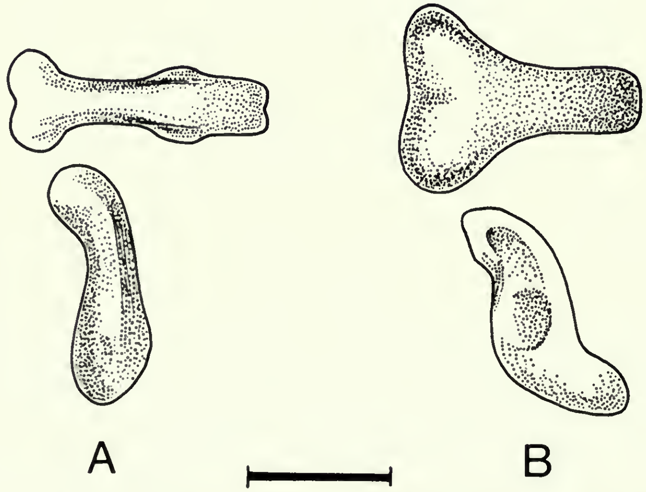


Fig. 8 Kinethmoid of A, *Zacco macrophthalmus*, B, *Barilius bola*, in dorsal and lateral views.

The *kinethmoid* is long and somewhat rod-shaped, its ventral tip articulating with the anterior vomerine notch. Its distal tip is slightly bifurcated and a ligament runs from each bifurcation to the tip of the maxillary. From either side of the kinethmoid shaft a ligament attaches to the dorsal rim of the maxillary (see p. 162).

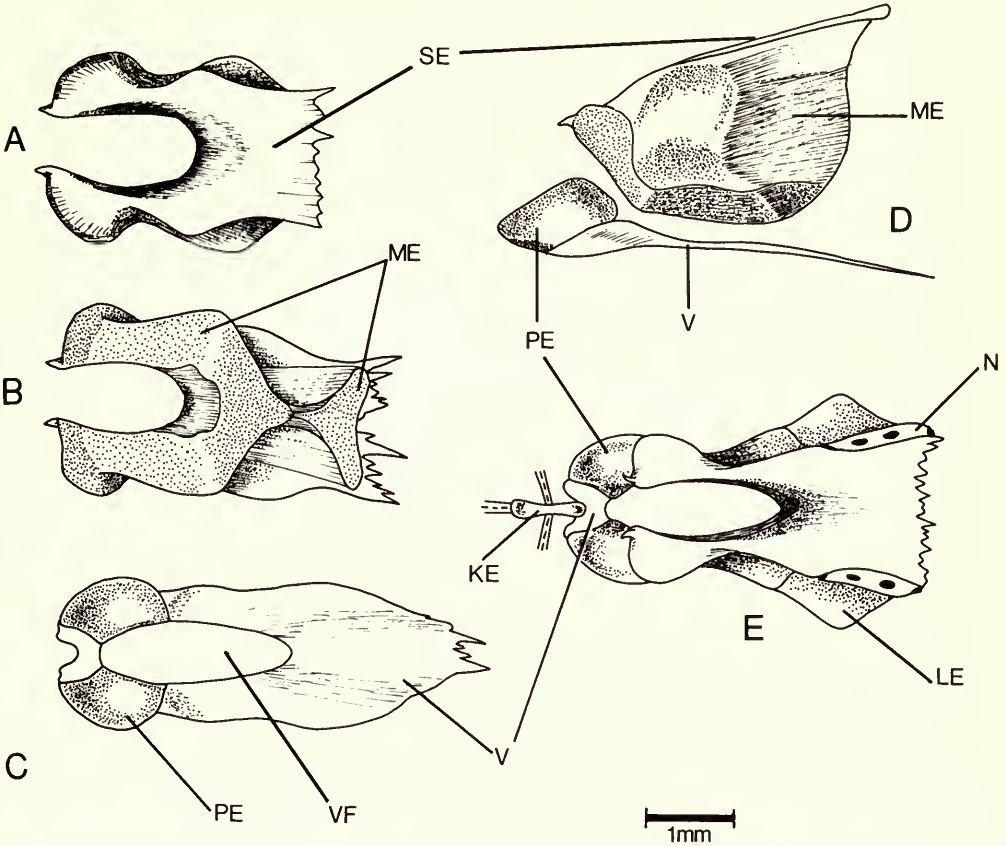


Fig. 9 *Engraulicypris sardella.* Ethmo-vomerine region. A, dorsal and B, ventral views of the ethmoid block. C, dorsal view of vomer. D, exploded lateral view of ethmo-vomerine block. E, dorsal view of entire ethmo-vomerine region showing articulation of the kinethmoid.

The *vomer* (Figs 9C & D) is short and broad, its posterior tip lying below the posterior border of the lateral ethmoids. The anterior half of the vomer is perforated by an ellipsoidal foramen (VF, Fig. 9C), the boundary of which coincides with the rim of the overlying ethmoid. The lateral border of the vomer is slightly raised to form a support for the preethmoid and its anterior rim is deeply notched.

Orbital region

Opsariichthys

The *orbitosphenoids* (Fig. 10) are deep, anteriorly expanded bones. Ventro-medially they are joined to form a thick interorbital septum which contacts the parasphenoid. The *pterosphenoids* (Figs 10 & 12) provide the walls of the optic foramen and the roof to the anterior part of the posterior myodome. Anteriorly each pterosphenoid is bordered by the orbitosphenoid, dorsally it is overlain by the frontal and posteriorly by the sphenotic and part of the prootic. The junction with the prootic is along a narrow medially directed portion of that bone which forms the dorsomedial wall of the trigeminofacialis foramen. Ventrally the pterosphenoid is produced into a narrow stem which contacts the medial face of the ascending lateral wing of the parasphenoid. The orbital face of the pterosphenoid bears a groove for the passage of the supraorbital nerve trunk. Ventrally the groove enters the *pars jugularis* of the trigemino-facialis chamber of the prootic. The posterolateral face of the pterosphenoid bears a deep concave fossa from which runs a tendinous sheet to underlie the *levator arcus palatini* muscle (PTSF, Figs 10 & 12). Part of the anterior hyomandibular fossa extends onto the dorsal surface of the pterosphenoid.

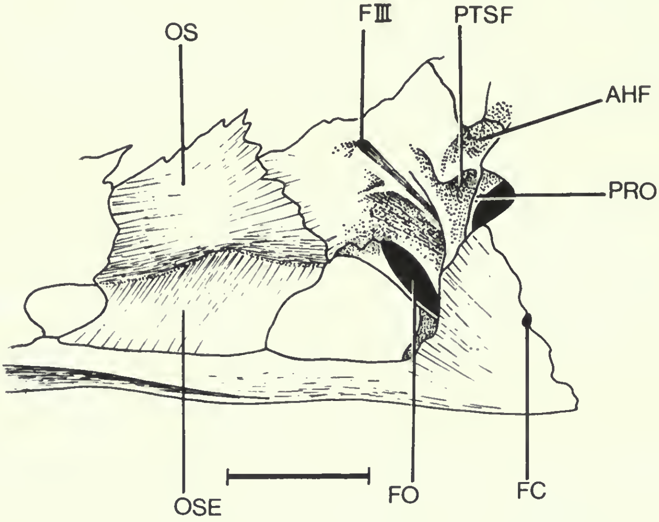


Fig. 10 *Opsariichthys*. Lateral view of orbital region.

The *parasphenoid* (Figs 11 & 12) is horizontally aligned, thin and grooved anteriorly where it overlies the vomer. On either side, posteriorly are ascending wings each of which contacts the pterosphenoid wing along a narrow front. The posterior dorsal edge of the wing is sutured to the prootic. This suture is interrupted by the carotid foramen (hypophysial foramen of Ramaswami, 1955). Below the prootic the parasphenoid widens to form a platform against which articulate the infrapharyngobranchials, the edges of this apophysis are formed by the prootics (parasphenoid platform of Howes, 1978). A prominent ridge runs along the ventral midline of the parasphenoid but becomes lessened posteriorly. The posterior ventral part of the bone is rounded and lies below the basioccipital.

Zacco

The *orbitosphenoid* differs from that of *Opsariichthys* in that it is much shallower and has a deeper interorbital septum. The *pterosphenoid* (Fig. 16) is much like that in *Opsariichthys*, bearing in its orbital face a deep furrow for the supraorbital nerve trunk. A major difference, however, is that the pterosphenoid does not articulate with any part of the parasphenoid but is sutured only to the medial projection of the prootic and, furthermore, there is no fossa in its posterolateral face.

The *parasphenoid* differs from that in *Opsariichthys* in being curved upward instead of horizontally aligned. The carotid foramen is greatly expanded in *Zacco* to form a large fenestra between the parasphenoid wing and the prootic (Fig. 16). The fenestra is partially covered by a fascia of tissue from which extends part of the *adductor arcus palatini* muscle. There is a moderately developed dorsal medial crest along the length of the parasphenoid but this never extends upwards to contribute to the interorbital septum stemming from the orbitosphenoids. As in

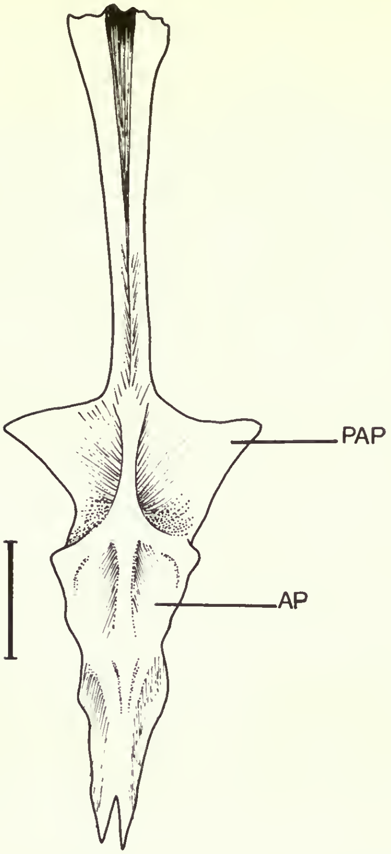


Fig. 11 *Opsariichthys*. Ventral view of parasphenoid.

Opsariichthys the parasphenoid bears a ventral groove for half its length. The apophyseal platform below the prootic is narrow and receives no contribution from the prootics.

Luciosoma

The *orbitosphenoid* is shallow and contacts the parasphenoid *via* a narrow interorbital septum. The *pterosphenoid* (Fig. 18) closely resembles that of *Opsariichthys* but whereas in that genus the bone forms the border of the anterior trigemino-facialis opening, in *Luciosoma* it is sutured without interruption both to the prootic and to the parasphenoid ascending process. There is a strong lateral ridge along the descending limb which makes contact with the parasphenoid and a shallow partially covered lateral fossa. Part of the anterior hyomandibular fossa extends onto the parasphenoid.

The *parasphenoid* ascending process contacts both the pterosphenoid and prootic. The carotid foramen is small, and the apophyseal platform is extensive with small lateral contributions from the prootics, features shared with *Opsariichthys*.

Barilius

Group A. There is some variation in the depth of the *orbitosphenoid* septum. The *pterosphenoid* contacts the *parasphenoid* ascending process across a very narrow front. In some species (e.g. *B. bendelisis*) contact between the two bones is almost prevented by the intrusion of a thin wedge from the prootic. There is no lateral pterosphenoid fossa, and the carotid foramen is sometimes extensive, as in *Zacco*. The posterior margin of the parasphenoid is deeply indented and does not extend to meet the posterior border of the basioccipital. Thus, there is a ventral opening leading into the posterior myodome (see pp. 146–147).

Group B. The *orbitosphenoid* septum is narrow as in *Opsariichthys*. In *Barilius bola* a shallow ridge runs along the lateral face of the orbitosphenoid, broadening posteriorly into a wide shelf continuous with that on the pterosphenoid. The *pterosphenoid* (Fig. 19) contacts the anterior edge of the prootic without interruption; its ventral edge is sutured to the ascending process of the parasphenoid. There is some variation in the extent of contact between these bones, being greatest in *B. bola* and *B. guttatus*. The anterior hyomandibular fossa extends onto the pterosphenoid. Although a fossa is present on the lateral face of the pterosphenoid, it is very shallow. The *parasphenoid* ascending processes are short, but with long dorsal borders contacting the pterosphenoids. There is a depression in the lateral ascending process for the insertion of the *adductor arcus palatini* muscle. The carotid foramen is reduced. The apophyseal platform is well developed and receives lateral contributions from the prootics.

Group C. The *orbitosphenoid* has a lateral shelf which is confluent with a similar feature on the pterosphenoid. The *pterosphenoid* (Fig. 17B) contacts the prootic medially as well as laterally and its connection with the parasphenoid is also medial across a very narrow spur of that bone. There is a cavernous fossa on the lateral face of the pterosphenoid (PTSF, Fig. 19A), it is of the basin-type like that in *Opsariichthys*, but is covered laterally so as to become a deep, conical chamber. The *parasphenoid* is wide anteriorly. Posteriorly its ascending process forms a wide connection with the prootic. The carotid foramen is reduced. The prootics contribute only marginally to an apophyseal platform. The parasphenoid does not provide a floor to the myodome.

Engraulicypris

The *orbitosphenoid* is produced into a long, shallow interorbital septum. The *pterosphenoid* (Fig. 22A) bears a deep lateral fossa (PTF) and it contacts the ascending process of the parasphenoid across a narrow front. The *parasphenoid* ascending process is high and broad with a lateral depression. Its otic portion is flat, with the posterior border deeply indented and not entirely flooring the basioccipital.

Otic region

Opsariichthys

The *prootic* (Figs 10 & 12) is the largest bone in the braincase. The lateral face bears a wide commissure covering the trigemino-facialis chamber. Anteriorly, contact is made with the pterosphenoid along a narrow surface just above the anterior opening of the chamber. Ventro-anteriorly the prootic is sutured to the ascending process of the parasphenoid. Ventrally, the prootic is flattened and contributes to the apophyseal platform formed on the lateral border of the parasphenoid. The posterior border of the prootic is contacted by the basioccipital and epioccipital. The postero-dorsal face of the prootic is depressed and forms part of the medial wall of the subtemporal fossa. Dorsally, the prootic is bordered by the autosphenotic and the autopterotic. The anterior and posterior hyomandibular fossae are confined to these two latter bones and do not invade the prootic. The medial face of the prootic bears a shelf extending from below the trigemino-facialis chamber to meet its partner from the opposite side in the midline and so forming the roof of the myodome (Figs 12 & 15). A large depression in the medial face of the prootic forms the cavum utriculus (Figs 12B–C).

The major part of the dilatator fossa lies in the *sphenotic* (Fig. 13) which is overlapped along its medial margin by the pterotic and the frontal. Anteriorly the bone extends laterally as a thin concave wall, the ventral surface of which forms part of the anterior hyomandibular fossa. Between the dorsal borders of the sphenotic and pterotic is a lateral temporal foramen. The

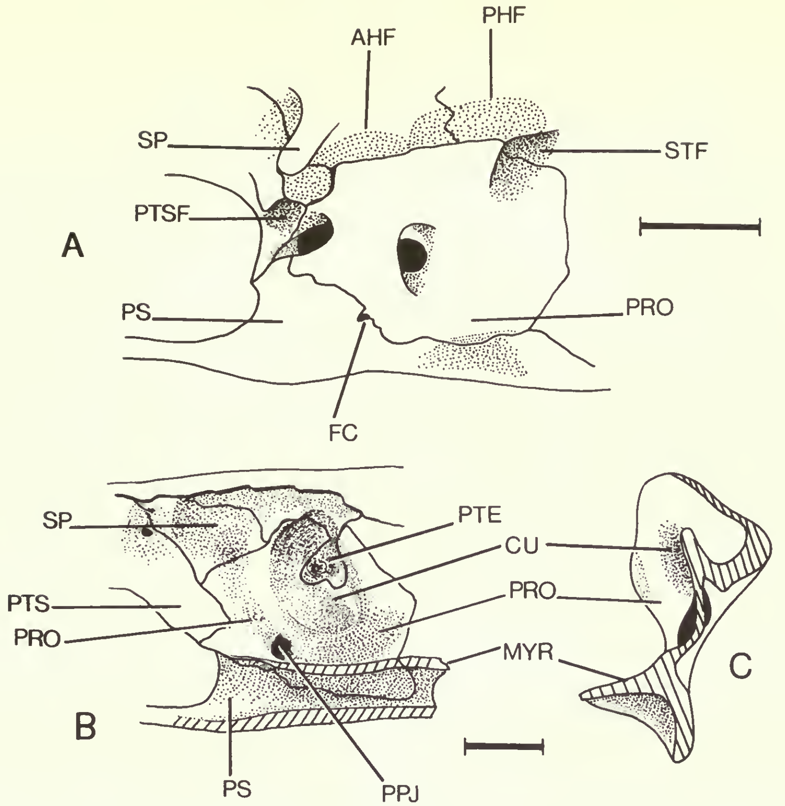


Fig. 12 *Opsariichthys*, otic region in A, lateral and B, medial views. C, cross-section through anterior part of the prootic.

lateral process of the sphenotic is sloped antero-ventrally, its dorsal surface is broad which narrows ventrally into a lamellar wall.

The *pterotic* (Figs 12–14) is bordered dorso-medially by the parietal and epioccipital, and dorso-anteriorly by the frontal and sphenotic. The exposed cranial surface of the pterotic is narrow. Ventrally it is sutured to the prootic and extends posteriorly as a thick limb terminating in a ventrally directed spine. The ventral border of the pterotic houses the greater portion of both hyomandibular fossae. The pterotic contributes to the lateral wall and roof of the subtemporal fossa and it also provides, posteriorly, the lateral wall of the posttemporal fossa. Medially this wall is perforated and opens into the subtemporal fossa; thus the subtemporal fossa is connected to the posttemporal fossa via an intrapterotic tunnel (PSFF, Fig. 13B). Epaxial muscle fibres run through this tunnel to insert along the lateral wall of the subtemporal fossa.

The *exoccipital* (EXO, Figs 13–15) is bounded dorsally by the epioccipital with which it forms the medial wall of the subtemporal fossa; anteriorly it is bordered by the prootic, and ventrally by the basioccipital. Ventrally, the exoccipital is slightly inflated to form part of the saccular recess, and laterally it is pierced by the foramen for the vagus nerve. Dorso-posteriorly, that part of the bone containing the semi-circular canal turns outward to contact the pterotic and the intercalar. The posterior portion of the epioccipital surrounds the lateral occipital foramen, its dorsal surface being bounded by the supraoccipital. Medially, a horizontal sheet of bone extends from each exoccipital to contact one another in the midline and so form the roof of the cavum sinus imparis.

The *lateral occipital fenestra* (LOC, Fig. 14) is covered by connective tissue which thickens around the border of the foramen. There appears to be no insertion of muscle fibres onto this tissue and it lies as a 'window' covered by epaxial musculature.

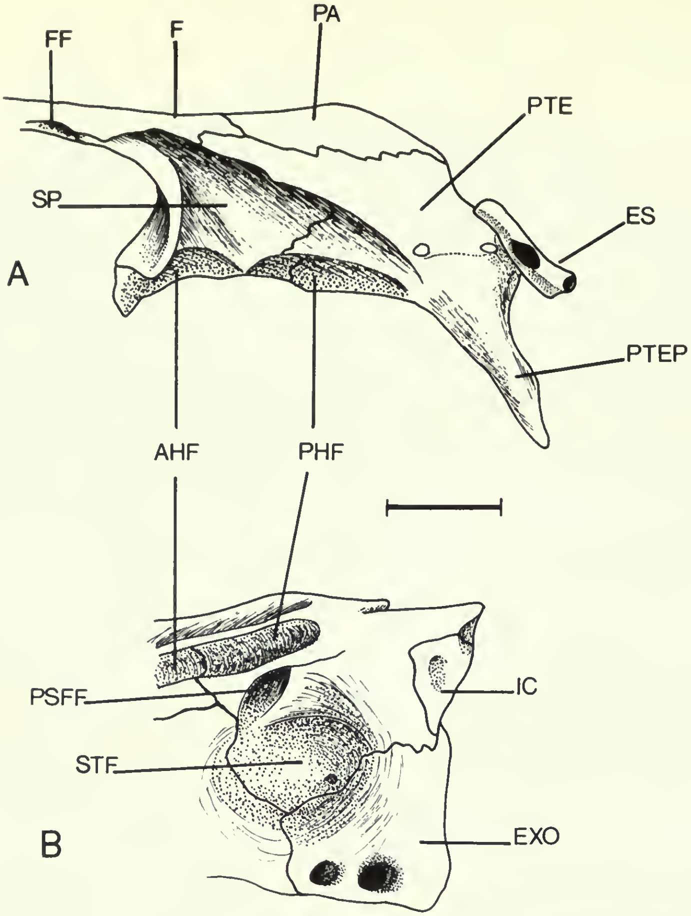


Fig. 13 *Opsariichthys*, pterotic region in A, lateral and B, ventral views.

The *epioccipital* (EPO, Fig. 14) is bordered medially by the supraoccipital, posteriorly by the exoccipital, anteriorly by the parietal and laterally by the pterotic. Its lateral face forms the upper medial wall and roof of the posttemporal fossa (PTF, Fig. 14). The dorsal surface of the epioccipital also contributes to the roof of the subtemporal fossa.

The *intercalar* (IC, Figs 13B & 14) is large and overlaps the suture between the exoccipital and the pterotic.

The *basioccipital* (BO, Fig. 15) is bordered dorsally by the exoccipital, anteriorly by the prootic and ventro-medially by the parasphenoid. Medially, each basioccipital contacts its partner to form the floor of the cavum sinus imparis and the roof of the posterior myodome (see below). The walls of the cavum sinus imparis are formed by dorsal extensions of each basioccipital on either side of the midline, the extension contacting the roof formed by the exoccipital (Fig. 15). Ventro-posteriorly there is a pharyngeal process which bears a high dorsal ridge; its ventral surface is expanded into a triangular masticatory plate (BOP, Fig. 15) which terminates in a high blade-like wing. The aortic foramen (AF) lies dorsal to the plate.

The *posterior myodome* (MYO, Fig. 15) extends far into the basioccipital. The basioccipital walls of the myodome converge to contact each other and seal the myodome posteriorly. In a specimen of 38·5 mm SL, however, the basioccipitals do not contact one another and the myodome is open posteriorly.

The *supraoccipital* (SO, Fig. 14) bears a medial ridge which runs backwards as a low lamellar

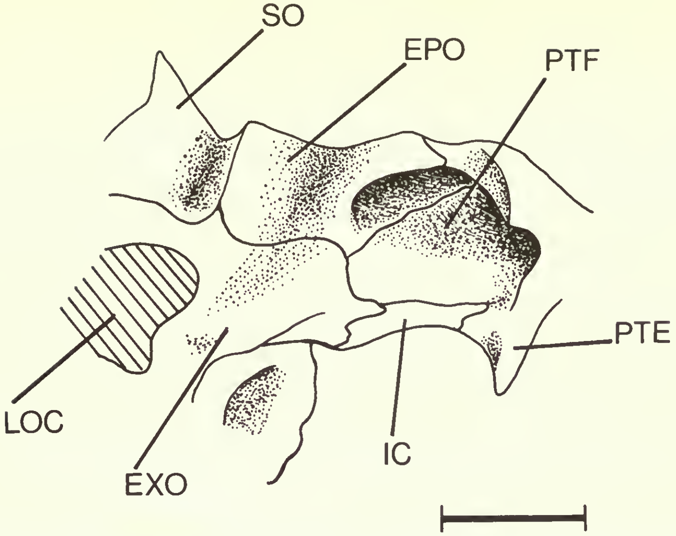


Fig. 14 *Opsariichthys*, pterotic region, right side, posterior oblique view.

process. Together with the epioccipitals, the supraoccipital forms a narrow post-parietal platform (see Howes, 1978).

Zacco

The *prootic* is of a similar shape to that in *Opsariichthys*, and likewise forms the border of the anterior foramen to the trigemino-facialis chamber. However, unlike *Opsariichthys* the lateral commissure is narrow, and the carotid foramen is greatly enlarged (Fig. 16). The *sphenotic* (Figs 16 & 17A) bears a thin lateral process which is curved ventro-posteriorly; its anterior face is deeply indented and provides a site of origin for part of the *levator arcus palatini* muscle. Only part of the sphenotic contributes to the dilatator fossa, the frontal forming the anterior part. The anterior hyomandibular fossa extends along the ventral surface of the sphenotic.

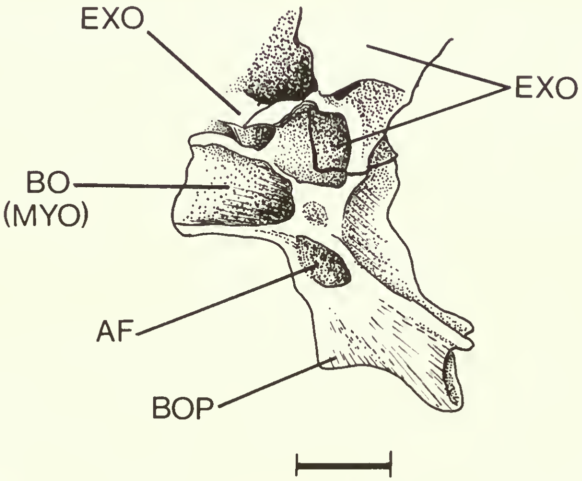


Fig. 15 *Opsariichthys*, basioccipital region cut through to show posterior myodome in anterior oblique view.

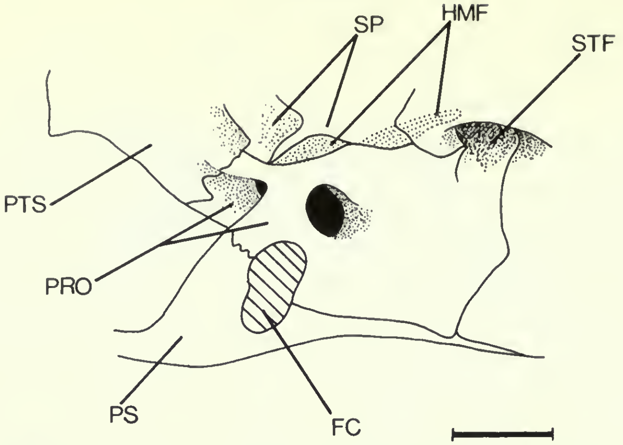


Fig. 16 *Zacco macrophthalmus* otic region in lateral view.

The posterior face of the *pterotic* forms the rear wall of the subtemporal fossa and the floor of the posttemporal fossa. There is no connection between the posttemporal and subtemporal fossae. The ventral surface of the pterotic houses the posterior hyomandibular fossa. The posterior process is of variable length and diameter, being thick and truncated in *Z. platypus* but slender and elongate in *Z. macrophthalmus* (PTE, Fig. 17A). The *basioccipitals* house part of the posterior myodome which is completely floored by the parasphenoid.

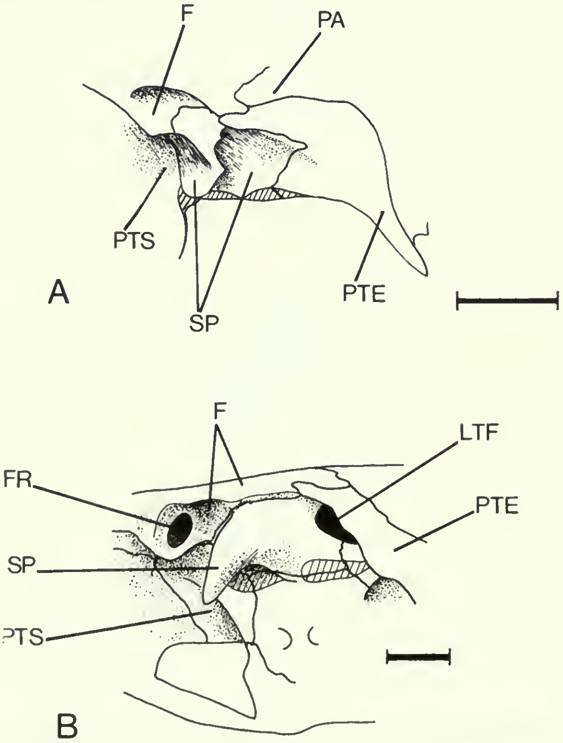


Fig. 17 A. *Zacco macrophthalmus* pterotic region, lateral view. B. *Barilius microcephalus* otic region, lateral view.

Luciosoma

The *prootic* is long and relatively shallow when compared with that in *Opsariichthys* and *Zacco* (Fig. 18). Contrary to the condition in those two genera, the anterior trigemino-facialis foramen is situated within the lateral face of the prootic, some way from its anterior border. The lateral commissure is wide. The *sphenotic* (Fig. 18) is long with a thick lateral process. The ventral surface of the bone bears the long anterior, and part of the posterior, hyomandibular fossa. The dorsal border of the sphenotic is sutured with the frontal and pterotic but neither of these bones forms a roof to the dilatator fossa.

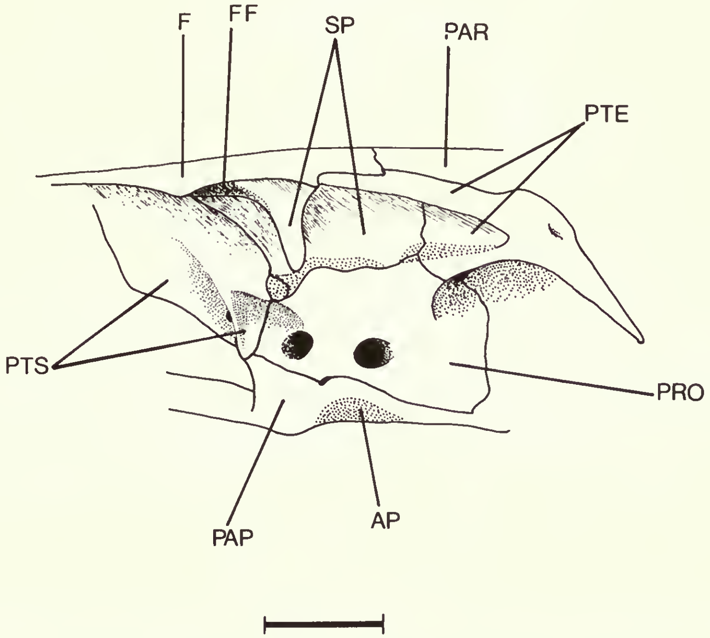


Fig. 18 *Luciosoma bleekeri* otic region, lateral view.

The *pterotic* (Fig. 18) is an elongate bone bearing the greater part of the posterior hyomandibular fossa on its ventral surface. The posterior process is long and spine-like but not so obliquely angled as in *Opsariichthys*. The pterotic forms the outer and posterior walls of the subtemporal fossa and part of the lateral wall of the posttemporal fossa which opens into it by way of an intramural channel. A *posterior myodome* is enclosed posteriorly by the basioccipitals and is floored ventrally by the parasphenoid. The *lateral occipital fenestra* is almost rectangular, a feature shared with some *Rasbora* species. There is no post-parietal platform and the *supraoccipital* crest is greatly reduced.

Barilius

Group A. The *prootic* resembles that of *Opsariichthys* and *Zacco* in that the anterior trigemino-facialis foramen is situated on the border of the bone. The *sphenotic* forms the major part of the dilatator fossa, its lateral process varies interspecifically from a thin lamella, as in *Opsariichthys*, to a stout spine. The posttemporal fossa contained in the pterotic is connected with the subtemporal fossa through a small foramen.

In some species of this group the posterior myodome is open ventrally so as to provide a passage for part of the eye musculature (see below, p. 147).

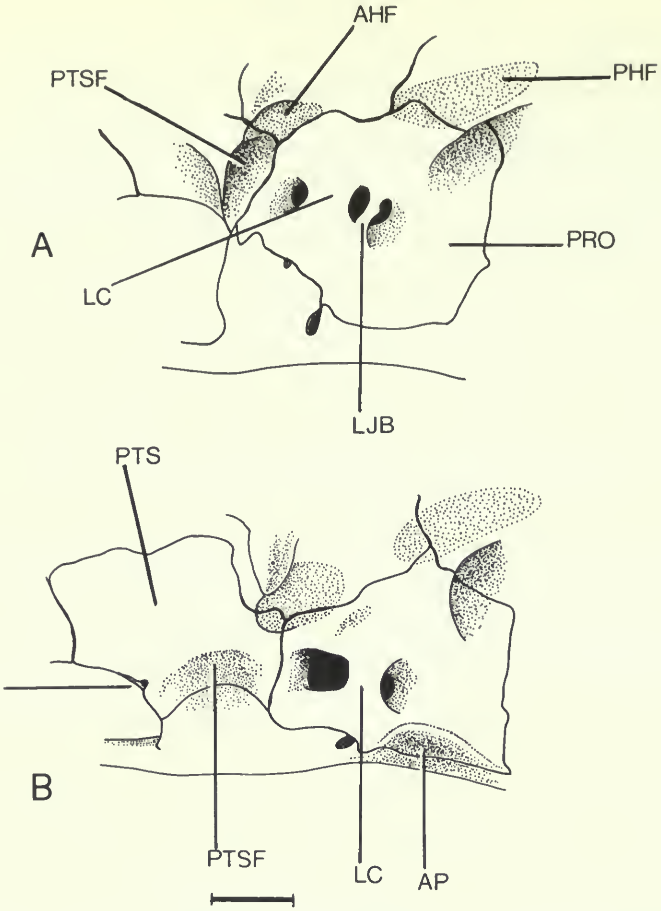


Fig. 19 Otic regions of A, *Barilius microcephalus* and B, *Barilius bola*, lateral views.

Group B (Fig 19B). The *prootic* bears the anterior trigemino-facialis foramen in its lateral face, and the lateral commissure is narrow. The carotid foramen is small. The lateral process of the *sphenotic* is a stout limb projecting either at right-angles or directed caudad. The anterior hyomandibular fossa is small and confined to the anterior ventral surface of the bone. There is no dilatator fossa, the lateral face of the sphenotic being almost perpendicular. There is a lateral temporal foramen shared between the sphenotic and pterotic. The *pterotic* does not provide a solid rear wall to the subtemporal fossa but is perforated by the greatly enlarged posttemporal foramen (see Howes, 1978). The posttemporal 'fossa' does not exist as an intramural channel as it does in *Opsariichthys*, *Luciosoma* and *Barilius Group A* species. The large subtemporal vault is roofed by the epioccipital and parietal and partly by the pterotic which also forms the lateral wall and posterior ventral bridge (Fig. 20).

The *posterior myodome* is open ventrally in the African species but closed in the two Asian representatives, *B. bola* and *B. guttatus* of this group. The form of the opening is similar to that described below in species of *Barilius Group C* but is not as extensive. A trend towards the closure of the myodome is apparent in various species of this group, the myodome being largely open in *B. loati* but the opening much reduced in *B. salmolucius*. This morphocline is correlated, as are other characters, with an elongation of the cranium (see p. 181).

Group C (Fig. 19A). The *prootic* is large and the anterior trigemino-facialis foramen is in its lateral face, the lateral commissure is long. The *sphenotic* is short but deep and bears an extensive

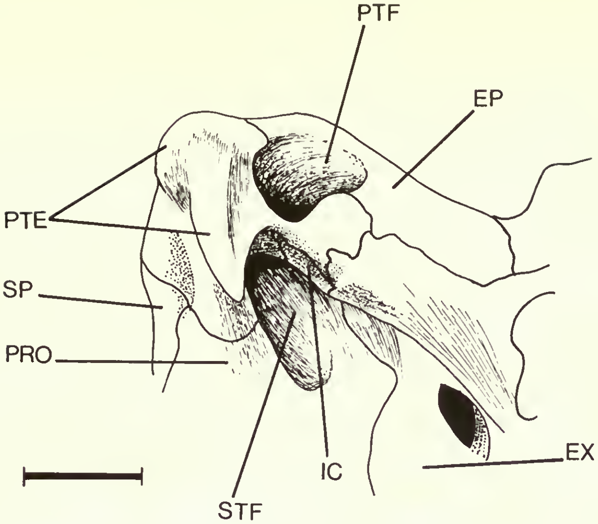


Fig. 20 *Barilius bola*. Ventral oblique view of posttemporal and subtemporal fossae.

lateral process. In *Barilius microcephalus* there is a large lateral temporal foramen, a feature shared with species of *Barilius Group B* and *Opsariichthys* (LTF, Fig. 17B & Howes, 1978 : 35). The ventral surface of the sphenotic contains part of the anterior hyomandibular fossa. The *basioccipital* is unfloored so that the *posterior myodome* is open ventrally (Fig. 21). The *recti inferioris* eye muscles extend from the medial edges of the basioccipital process to enter the myodome; the *recti exterioris* originate from the prootic walls of the myodome. This feature is discussed further below, p. 153.

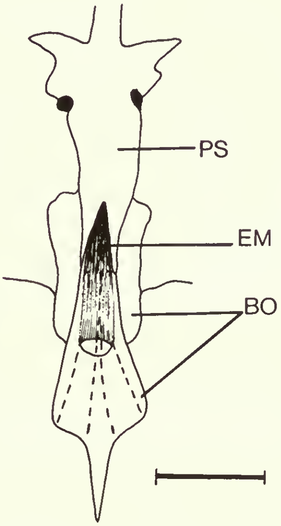


Fig. 21 *Barilius microcephalus* otic region seen ventrally. Dashed lines indicate path of the eye muscles through the myodome.

Engraulicypris

The *prootic* (Fig. 22A) is of similar shape to that in *Luciosoma*. The anterior trigemino-facialis foramen is situated in the lateral face of the bone, the lateral commissure is narrow and there is a deep jugular groove crossed by a narrow spur. The *sphenotic* (Figs 22 & 23) bears a broad, ventrally directed lateral process. Its dorsal surface forms the major portion of the dilatator fossa and ventrally bears the anterior hyomandibular fossa.

The *pterotic* (Figs 22–24) has a broad cranial surface and a short, stout, posterior process. Its medial face forms the lateral wall of the subtemporal fossa which is perforated by a small foramen leading into the posttemporal fossa (Figs 22 & 24); no muscle element passes through into the subtemporal fossa. The *basioccipital* is unfloored so that the posterior myodome is open ventrally (Figs 22 & 23). The *recti inferioris* eye muscles extend from a notch in the ventro-lateral border of the bone to enter the myodome. The basioccipital process is very short with a ventral channel and the masticatory plate is weakly developed.

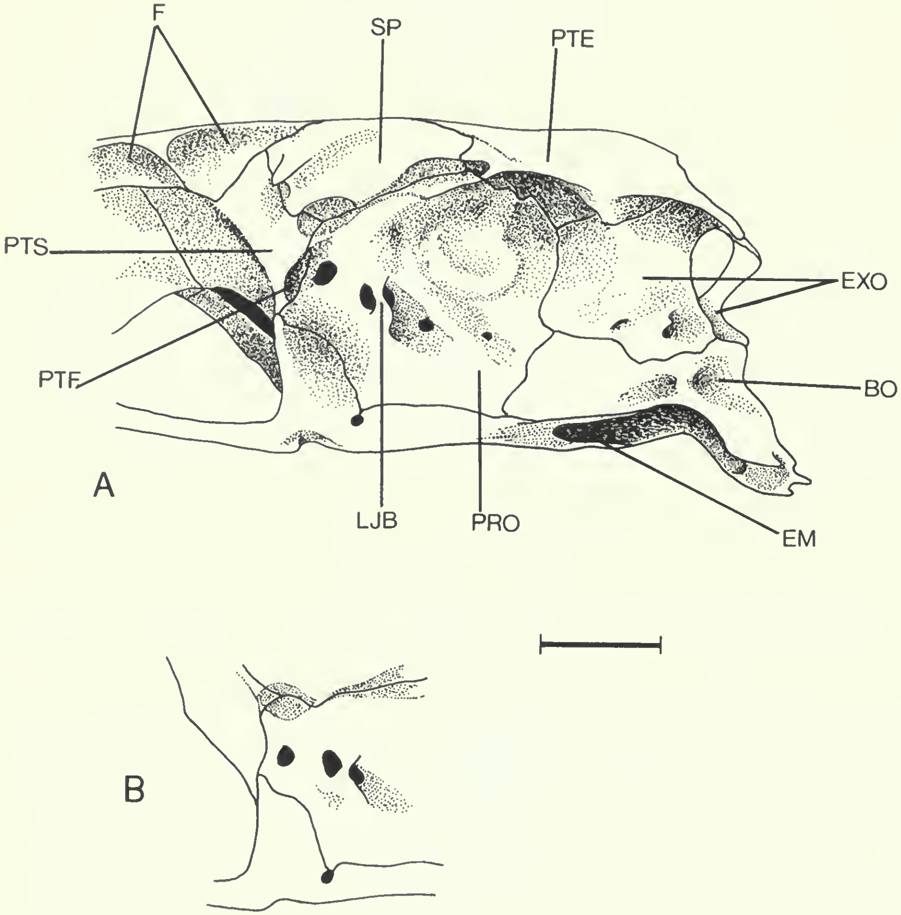


Fig. 22 A. *Engraulicypris sardella* neurocranium, ventro-lateral view. B. *Barilius* (=*Leptocypris*) *niloticus* otic region, lateral view.

Comments on the neurocranium

The broad, shallowly notched ethmoid block which is characteristic of *Opsariichthys* is a feature shared with *Luciosoma* and *Barilius* species of *Groups B* and *C*. This broad type of ethmoid appears to represent a plesiomorph condition amongst the Cyprinidae. In the various groups investigated so far, it is the most plesiomorph members which possess a wide, shallowly notched supra-ethmoid-mesethmoid and a vomer that protrudes little beyond the anterior ethmoid border (see Howes, 1978). With elongation of the cranium and jaws, there is seen a correlated narrowing of the ethmoid and a posterior elongation of the anterior notch. Such a morphocline can be found

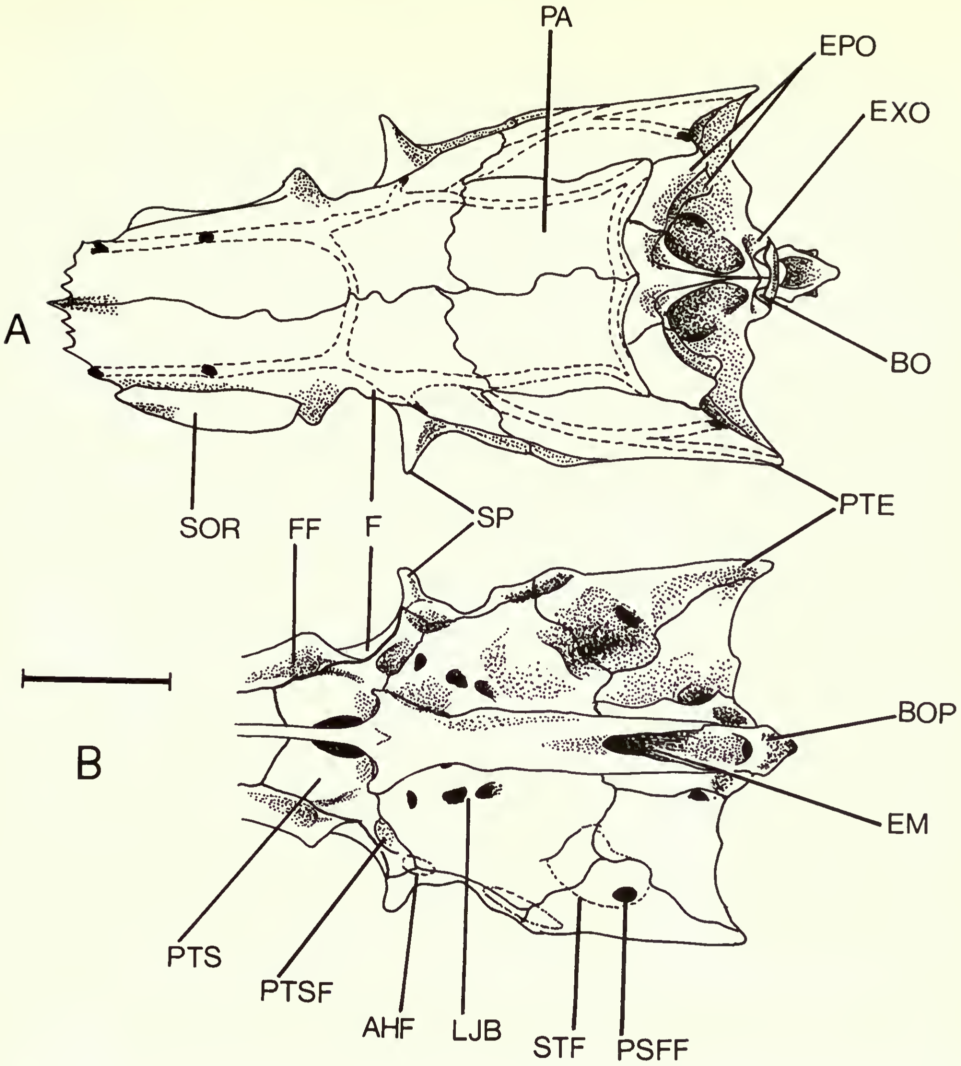


Fig. 23 A. *Engraulicypris sardella* cranium in A, dorsal and B, ventral views. The left side is unshaded for clarity and the limits of the various fossae are indicated by dotted lines.

in the cultrines (*Culter–Erythroculter*), aspinines (*Aspius–Luciobrama*) and hemicultrines (*Xenocypris–Ochetobius*). (In barbines and labeoines, the most derived members of the respective groups possess a medial elongation of the ethmoid block. This is presumably an adaptation involved with the inferior position of the mouth.)

In the taxa reviewed in this paper, the dorsally excavated supraethmoid of *Luciosoma* is considered apomorphic. A similar ethmoid morphology is found in some *Rasbora* species (see p. 183). The thickened vomer of *Opsariichthys* and *Barilius Groups B* and *C* is also considered a synapomorphy (see Howes, 1978).

The ethmoid region of *Engraulicypris sardella* is highly derived, its modification making for a highly protrusile jaw mechanism (see p. 164). In this respect it shares no feature with any of the genera described above.

The preethmoids of *Opsariichthys*, *Zacco*, all *Barilius* and *Luciosoma* are large and articulate with the palatine. This is presumably the plesiomorph condition for in those taxa which show cranial elongation the preethmoids are reduced in size and in some hemicultrines (e.g. *Ochetobius*) the palatine no longer articulates with the preethmoid but has moved posteriorly so as to contact the edge of the mesethmoid.

There is no anterior myodome in any of the genera discussed here.

A character which appears to have some significance as an indicator of relationship amongst the genera under discussion is the connection between the pterosphenoid, parasphenoid and prootic. In *Opsariichthys*, *Luciosoma*, some species of *Rasbora*, all *Barilius* and *Engraulicypris* there is some connection (either medial or lateral or both) between the pterosphenoid and the ascending wing of the parasphenoid. In an earlier paper (Howes, 1978) I stated that in some species of *Barilius* the pterosphenoid did not contact the parasphenoid. Having now re-examined all the specimens used in that study I find that there is such a connection, albeit a slight one in some cases. An exception is in *Zacco* where the pterosphenoid has no connection with the parasphenoid.

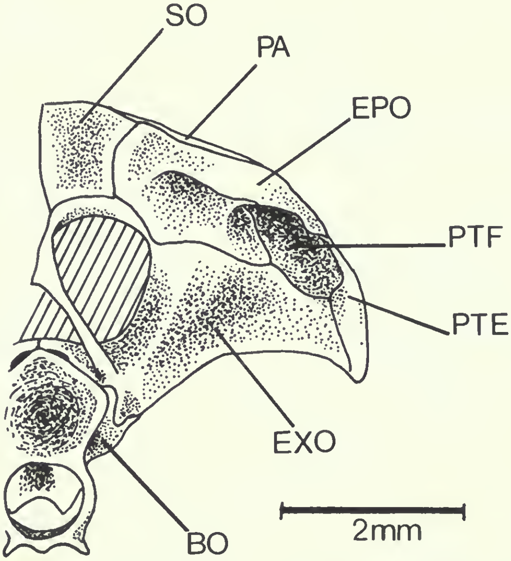


Fig. 24 *Engraulicypris sardella* cranium, posterior view of left side.

An associated character is the position of the anterior foramen of the trigemino-facialis chamber. In all genera apart from *Luciosoma*, *Engraulicypris* and *Barilius Groups B* and *C* it is formed by the anterior border of the prootic, but in the exceptional taxa the foramen is situated within the lateral face of the prootic.

In order to determine the significance of these features a morphological survey was made of the otic region in the Cyprinidae; the following 'classification' emerges.

Type 1. Pterosphenoid makes no contact with the parasphenoid; the anterior trigemino-facialis foramen is formed by the anterior border of the prootic; lateral commissure variable in length; myodome of variable depth; hyomandibular fossa sometimes invades the pterosphenoid.

Type 2. Pterosphenoid contacts the medial face and a narrow dorsal area of the parasphenoid wing; the anterior trigemino-facialis foramen is formed by the anterior border of the prootic; lateral commissure wide; myodome deep; hyomandibular fossa extends on to the pterosphenoid.

Type 3. Pterosphenoid contacts the dorsal border of the parasphenoid wing; the anterior trigemino-facialis foramen is situated within the lateral face of the prootic; lateral commissure narrow; myodome shallow; hyomandibular fossa does not invade the pterosphenoid.

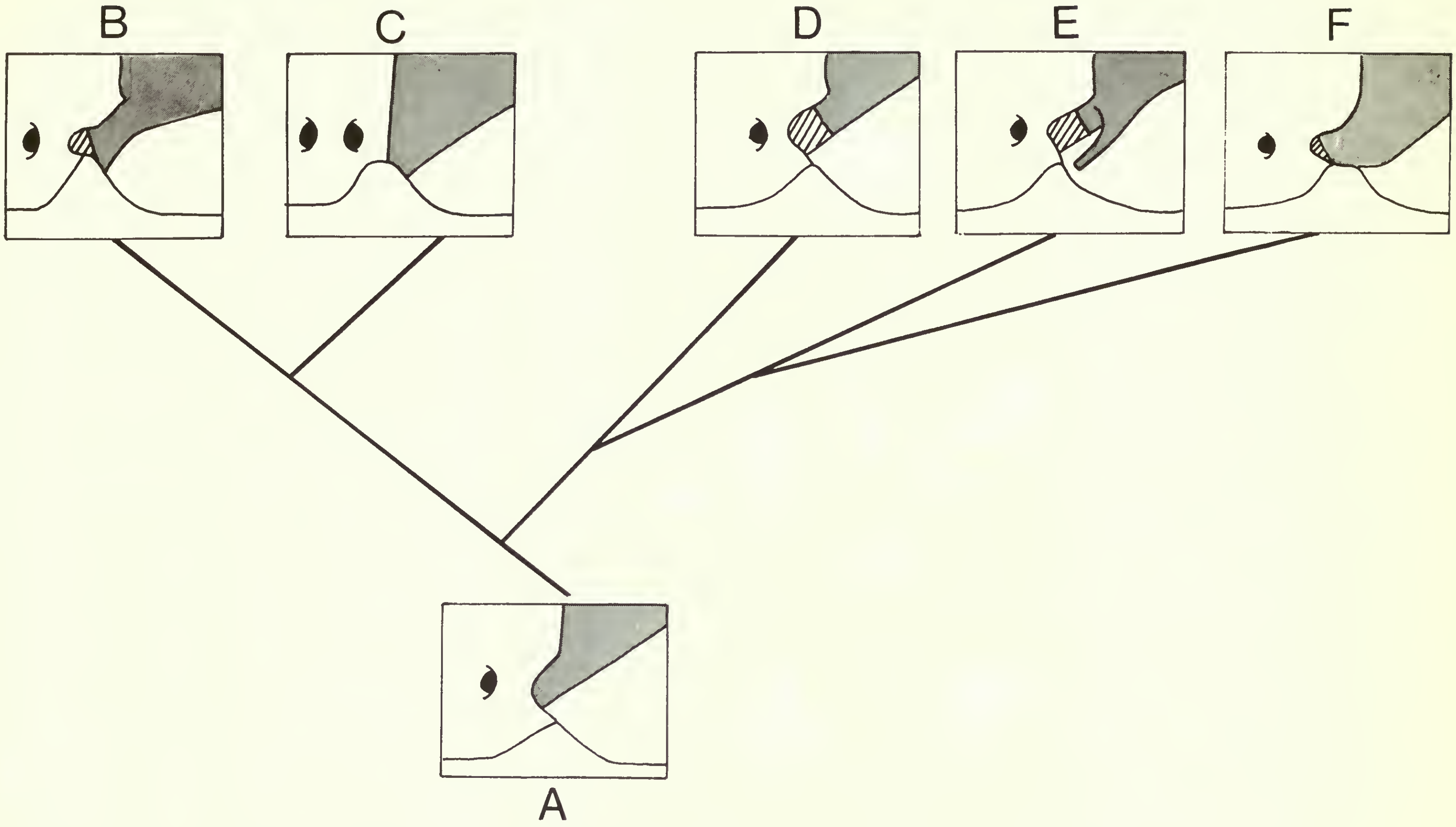


Fig. 25 Schematic diagram of the pre-otic neurocranium illustrating the possible derivation of four major morphotypes. A. Assumed ancestral type. B. Type 2 (*Opsariichthys*). C. Type 3 (*Barilius bola*). D. Type 1 (*Carassius*). E. Type 1 (*Rutilus*). F. Type 4 (*Oreoleuciscus*). The medial part of the prootic is cross-hatched, the pterosphenoid darkly shaded.

Type 4. As type 3 but the anterior trigemino-facialis foramen formed by the anterior border of the prootic and the hyomandibular fossa invades the pterosphenoid.

Type 5. Pterosphenoid contacts the parasphenoid *via* a medial parasphenoid process; lateral commissure excessively narrow; myodome reduced; the pterosphenoid does not bear the anterior hyomandibular fossa.

This classification is a basic one and a degree of intermediacy exists between the five types.

Type 1 appears to be the plesiomorph condition on the basis of the following evidence: (*a*) It is the type of contact found in members of those cyprinid groups so far investigated which are considered plesiomorphic on other grounds. (*b*) In juvenile specimens of *Opsariichthys* (*c*. 40 mm SL) the pterosphenoid fails to contact the parasphenoid and the ascending parasphenoid wing projects anteriorly as a small spur. During ontogeny a ventro-lateral process of the pterosphenoid contacts the parasphenoid spur. (*c*) In the characoids and presumed 'primitive' teleosts (i.e. Elopiformes) there is no contact between the parasphenoid and pterosphenoid.

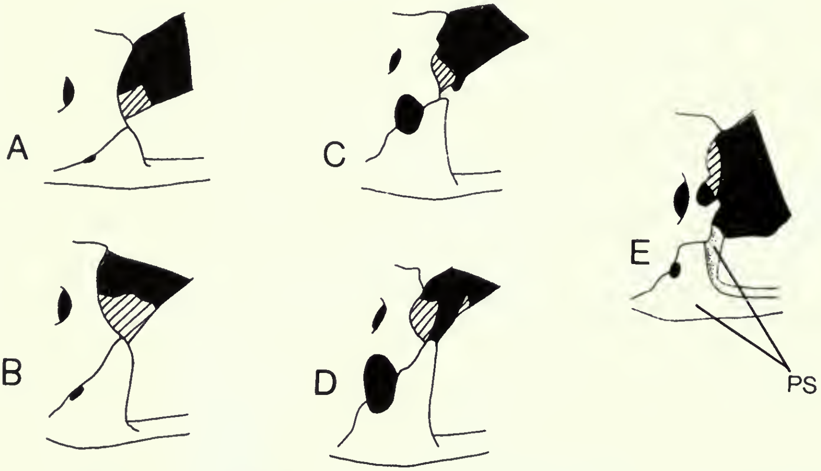


Fig. 26 Semi-diagrammatic drawings of the pre-otic neurocranium of A. *Cyprinus*. B. *Catla*. C. *Rutilus*. D. *Alburnus*. E. *Labeo*. The medial part of the prootic is cross-hatched, the pterosphenoid darkly shaded.

As well as being present in *Zacco* and *Barilius Group A*, Type 1 morphology is characteristic of *Cyprinus*, *Carassius*, *Catla* and *Xenocypris* (Figs 25D; 26A & B).

A derived condition of Type 1 is present in *Leuciscus* and *Rutilus* where a lateral strut of the pterosphenoid extends ventrally but does not make contact with the parasphenoid wing (Fig. 26C). However, in *Alburnus*, *Abramis*, *Squaliobarbus*, *Capoetobrama*, *Oreoleuciscus*, *Barbus intermedius* and some other taxa such a strut extends to join the parasphenoid (Fig. 26D).

Rognes (1973) described in labrids a strut extending from the pterosphenoid to the prootic; this he termed the 'internal jugular bridge'. Rognes (1973) illustrated variable conditions in the development of this strut which did not always contact the prootic. No link with the parasphenoid was described. Greenwood (1976) also described an internal jugular bridge in centropomids and again illustrated the variability of contact – only in one case was there found to be a direct pterosphenoid/parasphenoid contact.

No such variability exists in any of the adult cyprinids examined and the 'incomplete' contact of the pterosphenoid spur and parasphenoid (e.g. *Rutilus*) or complete contact (*Abramis*) are taxon-defining characters.

Type 2 morphology is confined to *Opsariichthys*. In this taxon the medial wall of the prootic does not extend beyond the anterior border of the parasphenoid wing, in contrast to the situation in Type 1 where the prootic extends well forward (cf. Figs 25B & D).

Type 3 morphology is confined to *Barilius Groups B, C*, *Engraulicypris* and *Luciosoma* (Fig. 25C); in no other taxa so far examined is the anterior trigemino-facialis foramen placed within the lateral face of the prootic. This is considered a derived condition and is seen as a 'sequential development' of Type 2.

Type 4 morphology appears to be a derived Type 1 condition in that there has simply been an elongation of the pterosphenoid and a lengthening of the parasphenoid wing. Numerous examples of this condition can be cited (e.g. *Barbus barbus; Schizothorax esocinus; Ochetobius elongatus; Erythroculter mongolicus; Elopichthys bambusa*) all of which are amongst the most derived members of their respective lineages in terms of cranial elongation (see comments on the ethmoid region, p. 149). This morphotype is best exemplified by *Oreoleuciscus* (Fig. 27). In this genus there is an extensive contact between the parasphenoid and pterosphenoid but an elongate fenestra exists between the pterosphenoid and the prootic, posterior to the parasphenoid ascending wing; the anterior trigemino-facialis foramen is also contained on the border of the prootic. (It is interesting to note that the closure of the pterosphenoid–prootic–parasphenoid fenestra would produce a condition approximating to that in *Barilius Group B*; *cf.* Figs 19B & 27.)

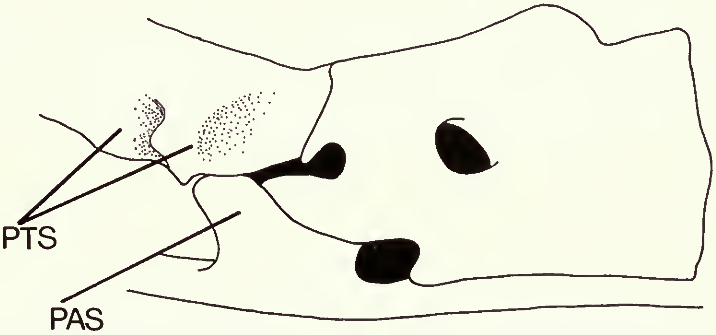


Fig. 27 Orbital-otic region of *Oreoleuciscus pewslowi*, lateral view.

Type 5 morphology has been encountered only in *Labeo*, *Barbichthys* and *Tylognathus* and is considered to be a derived condition (Fig. 26E).

A seemingly derived character shared by *Zacco* and *Barilius Group A* is the enlarged *carotid foramen* between the prootic and parasphenoid. This feature is also found in *Cyprinus*, *Rutilus* and *Abramis*. The common condition in the Cyprinidae is a small carotid foramen.

Mention should be made here that Vanderwalle (1974) considers the trigemino-facialis chamber of *Gobio* to represent a 'derived' condition because the jugular vein is not enclosed within a separate channel or tunnel. I have not found such an enclosure in any cyprinid examined, although in *Engraulicypris*, *Leptocypris* and some species of *Barilius Group C* there is a deep jugular groove along the lateral face of the prootic. Associated with this feature is a thin bridge of bone (LJB, Figs 19A; 22A & B; 23) crossing the posterior foramen of the pars jugularis and serving to separate the jugular from the trigemino-facialis nerve bundle. In some species of *Barilius* this bridge is incomplete and developed only as a thin process arising from the ventral part of the groove. A similar lateral jugular bridge occurs in alburnines and cultrines. Until the distribution of this feature is more fully documented for the cyprinids, no polarity can be ascribed to it.

The *pterotic*, when viewed dorsally, in *Opsariichthys*, *Luciosoma*, *Engraulicypris* and *Barilius Groups B* and *C* is seen to extend well posteriorly, whereas in *Zacco* and *Barilius Group A*, the posterior margin of the bone is truncated (Fig. 28).

A ventrally open *posterior myodome* is a feature of *Barilius* species in *Group A*, *B* and *C*. The only other cyprinid genera in which I have found an open myodome are *Leptocypris* and *Engraulicypris sardella*. Likewise, in those taxa the morphology of the eye muscles associated with the myodome is similar to that in *Barilius* (see p. 147). A ventro-posteriorly open myodome is present in several groups of characoids, and in these too some of the eye muscles originate from outside the myodome, the most specialized condition being found in the bryconines, acestrorhynchines and some characinines (pers. obs.). An open myodome and externally originating eye muscles also occurs in clupeoids, salmonids and some elopids. Patterson (1975) gave an account of the possible phylogenetic history of the posterior myodome, believing the open myodome to be a derived condition. Verraes (1976) showed that in *Salmo* the myodome opens during ontogeny and the eye muscles extend posteriorly through it. Thus, it would seem that the open myodome in cyprinids must be thought of as a derived state and synapomorphic for those genera possessing it. It was noted (p. 142) that in a small specimen of *Opsariichthys* the myodome was open, but closed during later ontogeny. Certainly the morphology of the posterior myodome in *Opsariichthys* differs quite considerably from that of other cyprinids in that the basioccipital is constricted below the lagenar capsule. Thus the posterior portion of the myodome is enclosed within the anterior part of the basioccipital, whereas in other cyprinids it extends to the posterior wall of the basioccipital. The same myodome morphology is apparent in the most derived species of *Barilius Group B* which suggests that the closed myodome is, as in *Opsariichthys*, secondarily derived, although I have been unable to ascertain whether in fact an open myodome occurs during ontogeny in these *Barilius* species.

The connection between the *subtemporal fossa* and *posttemporal fossa* is a feature common to all the genera presently under consideration with the exception of *Zacco*. This character has also been found in *Leptocypris* and in some species of *Rasbora;* its occurrence in these genera is discussed later (p. 180). As no other cyprinid taxon examined has such a connection between the fossae, this character is considered to be a synapomorphy.

Dermal bones of the skull

Opsariichthys

The *frontals* (F, Fig. 28) are broad and short with an irregular midline suture. The lateral border of each frontal is markedly concave where it contacts the supraorbital. Medial to its suture with the sphenotic there is a deep ridge from which stems the anterior part of the *levator arcus palatini* (FF, Fig. 13A). The frontal slightly overhangs the sphenotic to form a medial roof to the dilatator fossa. It contacts the pterotic across a narrow area.

Each *parietal* (PA, Figs 13 & 28) is broad and short (contained 4 times in the length of the frontals) with an irregular midline suture. The lateral border contacts the pterotic and the posterior border, the epioccipital and supraoccipital. The posterior border of the parietal is marked by a deep ridge through which runs the laterosensory canal. Each *nasal* (N, Figs 1–3) is small with a single dorsal opening. The *supraorbital* (SOR, Fig. 29) is very wide and does not contact the 5th infraorbital, the bones being separated by the outward curvature of the frontal. The 1st, 2nd, 3rd and 4th *infraorbitals* are large bones (Fig. 29). The 3rd and 4th do not cover the cheek but leave a naked area between their posterior borders and the preoperculum. The 5th infraorbital is reduced and contacts the pterotic.

Zacco

The *frontals* are narrow anteriorly and their lateral margins are gently concave (Fig. 28B). The *parietals* are broad and short, their posterior margins truncated. The *supraorbitals* are long and narrow. The 1st *infraorbital* is deep, the 2nd and 3rd shallow, 4th deep, and 5th reduced to an ossification around the sensory canal; it does not contact the supraorbital. There is interspecific variability in the size of the infraorbitals which are deeper and longer in *Zacco macrophthalmus*, *Z. temmincki*, *Z. barbatus* and *Z. pachycephalus* than in *Z. platypus*.

Luciosoma

The *frontals* are broad and long, with their lateral margin gently concave. As in *Opsariichthys* there is a deep frontal fossa (FF, Fig. 18). A particular feature of *Luciosoma* is a deep channel between the anterior opening of the frontal sensory canal and the posterior opening of the nasal

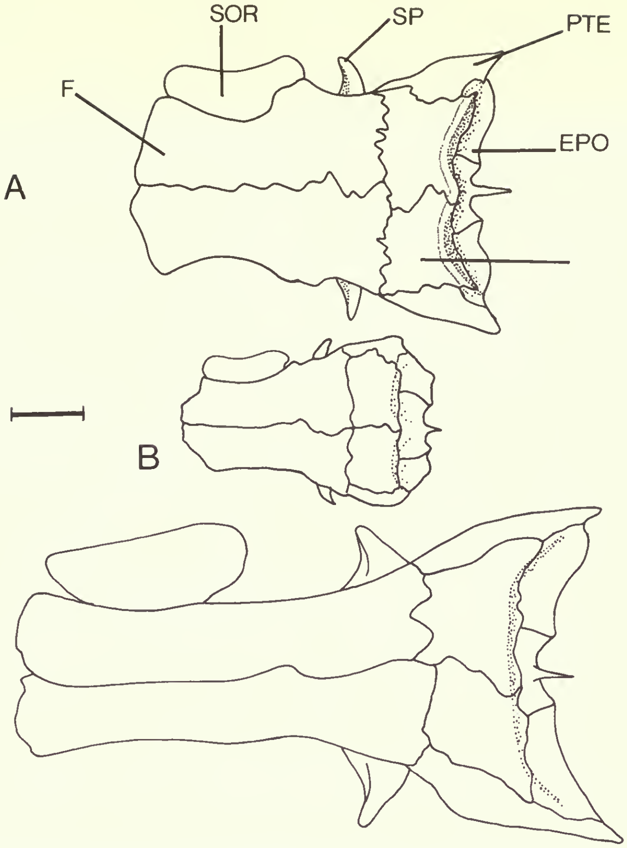


Fig. 28 Cranial roof of A. *Opsariichthys*. B. *Zacco platypus*. C. *Barilius bola*.

canal (FG, Fig. 6A). The *nasal* is short without a central dorsal pore (Fig. 6A). Each wide *supraorbital* contacts the 5th infraorbital. The 1st and 2nd *infraorbitals* are shallow, the 3rd expanded to almost cover the cheek, the 4th and 5th long.

Barilius

Group A. The *frontals* are narrow as compared with *Opsariichthys*, their lateral margin gently concave. The dilatator fossa deeply indents the postero-lateral margin of each frontal. The *parietals* are long, varying interspecifically from 2·5 to 2·8 times in the length of the frontals (cf. 3·8–4·0 in *Opsariichthys* and in other *Barilius* groups). The *nasals* are elongate each with 2 dorsal pores. The 1st and 2nd *infraorbitals* are shallow, the 3rd, 4th and 5th expanded (Fig. 29B). The 5th infraorbital contacts the narrow *supraorbital*.

Group B. The *frontals* are elongate and narrow, their lateral margin gently concave where the supraorbital joins. The *parietals* are slightly longer than those of *Opsariichthys* (3·8 times in frontal length) and their posterior lateral margins are extended (Fig. 28C). The 1st and 2nd *infraorbitals* are deep, the 2nd being elongate. The 3rd, 4th and 5th infraorbitals are expanded so as to cover the entire cheek region and contact the preoperculum (Fig. 29C); the 5th contacts the broad *supraorbital*.

Group C. The *frontals* are elongate but broader than those in *Group B*. In *Barilius microcephalus* the ventral frontal fossa is perforated so as to form a lamellar ring (FR, Fig. 17B). Part of the *levator arcus palatini* originates from the ventral surface of the frontal anterior to the ring, the muscle passing through it to join its other section which originates from the deep fossa dorso-posteriorly to the ring. In other species included in the group there is a deep frontal fossa similar

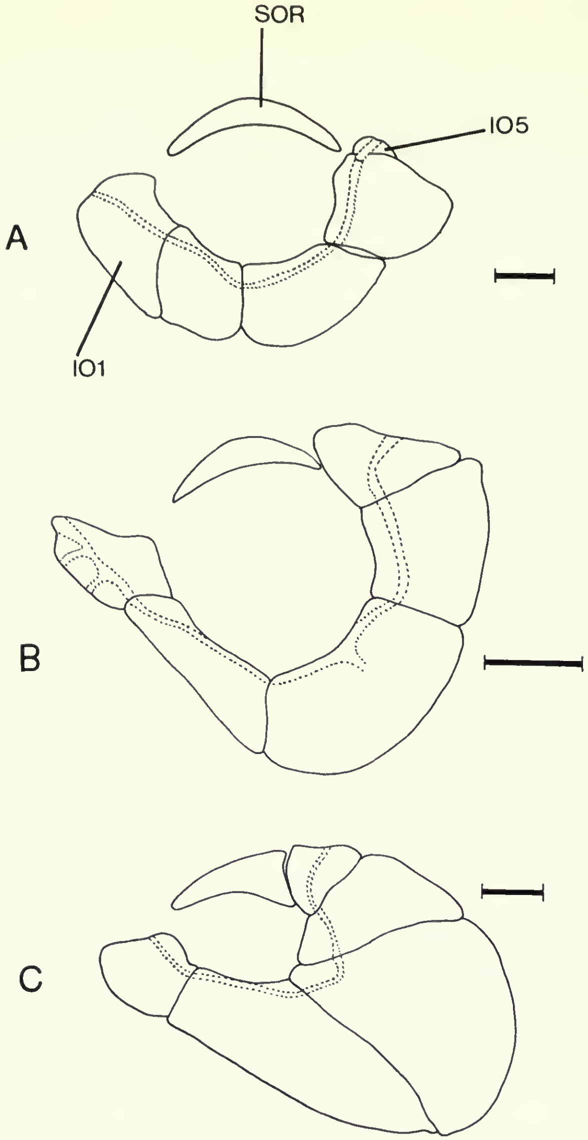


Fig. 29 Circumorbital series of A. *Opsariichthys*. B. *Barilius barila*. C. *Barilius bola*.

to that in *Opsariichthys* (see above). The arrangement of the circumorbital bones is like that in species of *Group A*.

Engraulicypris

The *frontals* (Fig. 23) are long and narrow and formed anteriorly into a shallow pit. The sensory canal contains a single pore midway along its length. Ventrally, each frontal bears a fossa which serves as a site for the origin of part of the *levator arcus palatini* muscle. The *parietals* are long, being contained twice in the length of the frontals. The *nasals* are elongate and curved so as to lie in the concavity of the ethmoid margin; each nasal has two dorsal pores. The *supraorbital* is long and broad and contacts the 5th infraorbital. The 1st infraorbital (Fig. 30) is extensive and when the jaws are retracted, it completely covers the maxilla and premaxilla. The posterior border is markedly concave and covers the anterior third of the 2nd infraorbital; the 3rd, 4th and 5th infraorbitals are long.

Comments
There is no contact between the supraorbital and the 5th infraorbital in *Opsariichthys* or *Zacco* but such contact is present in *Luciosoma*, *Engraulicypris* and all groups of *Barilius* and in these taxa the infraorbitals are expanded.

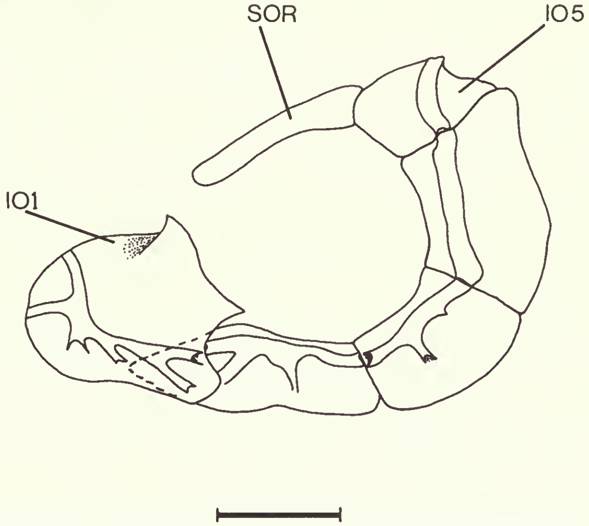


Fig. 30 Circumorbital series of *Engraulicypris sardella.*

In the majority of cyprinids the infraorbitals are reduced, presumably a secondary regression from an expanded ancestral condition (Tretiakov, 1946). In some groups such as the aspinines, where there has been elongation of the cranium, the infraorbitals are reduced to the canal-bearing part of the bone, whereas in the long-headed bariliines the infraorbitals are expanded. This condition appears to be due in part to the lateral expansion of the cranial musculature in bariliines, as evidenced by the produced sphenotic processes (Fig. 28C) and the need for a protective shield (p. 158). In the case of *Barilius Group B* (Fig. 29C), it appears that the expansion of the infraorbitals is a derived condition. This is clearly seen in the excessively elongate 2nd infraorbital and the pronounced orbital narrowing of the 3rd. Indeed, a transformation series of this character state can be witnessed in species of *Group B* and the more extreme forms of this morphocline are represented in various bariliine genera (see Figs 29A–C) where *Opsariichthys* represents the plesiomorph state and *Barilius bola* the derived.

Ramaswami (1955) has already commented on Regan's (1911) statement that *Opsariichthys* has a '... complete series of circumorbitals'. Ramaswami thought Regan's use of the word 'complete' ambiguous. Regan may have been referring to a series without interruption, in other words he believed there to be a contact between the 5th infraorbital and the supraorbital. The separation is only a narrow one and the interposing frontal could be mistaken for part of the supraorbital.

A *frontal fossa* is present in all the genera under discussion with the exception of *Zacco*. In *Opsariichthys* and *Luciosoma* the fossa is shallow and serves to support the *levator arcus palatini* muscle. In *Barilius Group A* the fossa is a deep anterior extension of the dilatator channel; in *Group C*, the fossa is also deep (and in *B. microcephalus* is penetrated by a foramen) but, as in *Opsariichthys* and *Luciosoma* it provides the site of origin for the *levator arcus palatini*. In *Barilius Group B* the frontal fossa has all but disappeared and exists only as a narrow ventral ridge. Apart

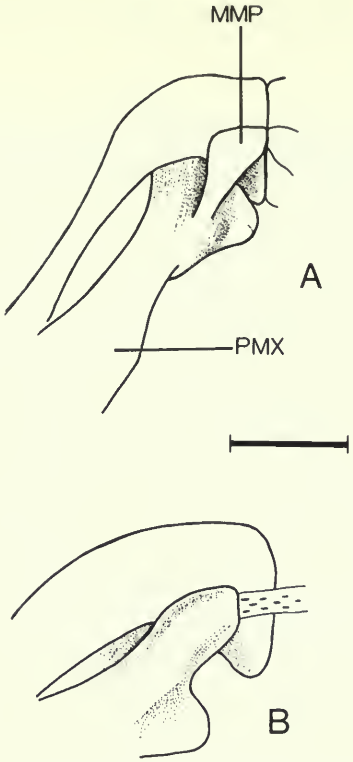


Fig. 31 Anterior of maxilla and premaxilla of A. *Opsariichthys*. B. *Zacco macrophthalmus*. Ventral views.

from *Leptocypris* and *Engraulicypris sardella* and some *Rasbora* species, I have not found any cyprinid with this type of frontal cavity. Many taxa, however, possess a sphenotic fossa, lying anteriorly to the sphenotic lateral process, from which the *levator arcus palatini* originates (e.g. *Zacco*, *Alburnus*).

Forey (1975) commented on a frontal ridge in clupeoids where it also serves as a site of origin for the *levator arcus palatini*. He also pointed out the apparent correlation between a frontal ridge and a hyomandibular process (see p. 165).

The jaw bones

Opsariichthys

The jaws have been described in some detail previously (Howes, 1978), therefore it is necessary here to note only the more pertinent features: The *premaxilla* is very slender with the anterior ascending process sloped backwards. The *maxilla* bears, antero-medially, an axe-shaped process which underlies the permaxilla and which contacts its partner from the opposite side along a narrow lateral face (Fig. 31A). The anterior tip of each maxilla extends almost to the symphysis of the premaxillaries (Fig. 32A). The *dentary* is deeply notched anteriorly and has a strong symphysial process. The ventral border bears 7–8 pores of the sensory canal. Posteriorly there is a high coronoid process, see Fig. 36E in Howes (1978).

Zacco

The *premaxilla* is a thick bone with a short ascending process. The anterior tips of each *maxilla* are widely separated from one another across the midline. Each anterior medial maxillary process is rounded distally and joined to its partner across the midline *via* a ligament (Fig. 31B). The *dentary* is shallow with a high coronoid process; a symphysial process is lacking.

In *Zacco pachycephalus* and *Z. barbatus* the jaws are like those in *Opsariichthys* in that (i) the premaxilla is thin and separated by a slight gap from the maxilla, (ii) the medial maxillary processes contact each other directly across the midline and not *via* a ligament and (iii) the anterior maxillary tips extend well forward.

Luciosoma

The *premaxilla* is exceedingly shallow, with a wide and short anterior ascending process which joins its partner to form an almost beak-like jaw. The *maxilla* is also shallow, overlapping the premaxilla for that bone's entire length. The anterior medial maxillary process is wide and contacts its partner along the midline. The outer anterior tip of the maxilla extends almost to the premaxillary symphysis (Fig. 32C). The *dentary* is shallow, with a short symphysial process. The lateral wall is curved outward as in *Opsariichthys* and the coronoid process is high.

Barilius

Group A. The *premaxilla* and *maxilla* are narrow, the former with a rather long ascending process and the latter with its anterior medial process making contact with its partner in the midline. The anterior tips of the maxillaries are widely separated from each other (Fig. 32B). The *dentary* is very shallow with a high coronoid process and there is no symphysial knob or anterior notch.

Group B. The jaws of *Barilius bola* are described in an earlier paper (Howes, 1978) and those of other species assigned to this group correspond in having shallow *premaxillaries* with short, wide, beak-like anterior ascending processes, shallow *maxillaries* each bearing a wide palatine notch and a wide medial anterior process. The anterior tip of each maxilla almost contacts its fellow across the midline (Fig. 32E). The *dentaries* are long and shallow with high coronoid processes and they lack symphysial knobs and anterior notches.

Group C. The jaws are closely similar to those of *Group B* except for deeper and shorter jaw bones and the tips of the premaxillary ascending processes being triangular instead of curved (Fig. 32D).

Engraulicypris

The *premaxilla* (Fig. 33C) has a short anterior ascending process, which is slightly indented in its leading edge, and a broad midlateral ascending process. The *maxilla* (Fig. 33A) bears a high, narrow midlateral ascending process from which extends a ligament to attach to the medial face of the 2nd infraorbital. The anterior tip of the maxilla is bifurcated, the medial process extending ventrally to contact its partner in the midline (Fig. 33B). The posterior part of the maxilla is rounded and expanded ventrally, this expanded portion is grooved so as to articulate with the dorsal posterior margin of the premaxilla. The *dentary* (Fig. 33D) is deep, with a short, broad, upright coronoid process, the posterior border of which is deeply concave. The *anguloarticular* is large with a long convex dorsal margin.

Hyopalatine arch

Opsariichthys

The *hyomandibula* possesses two articular heads separated from each other by a shallow depression. The anterior facet has a long sloped face which abuts against the pterosphenoid wall of the articulatory fossa. The posterior facet has a narrow surface which fits into the channel-like pterotic fossa. The anterior border of the hyomandibula is rounded below the anterior facet and

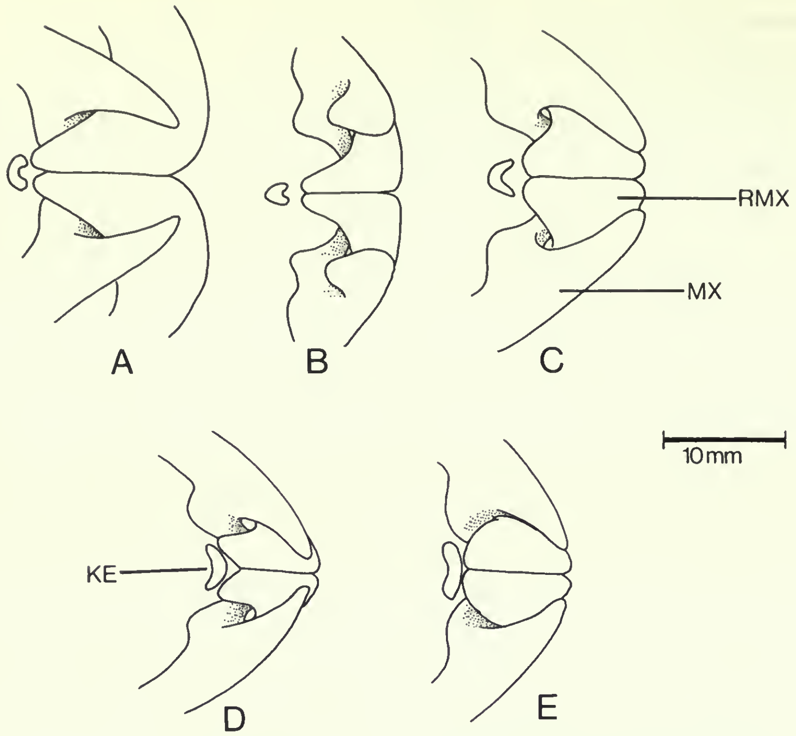


Fig. 32 Anterior of maxilla and premaxilla of A. *Opsariichthys*. B. *Barilius barila*. C. *Luciosoma bleekeri*. D. *Barilius microcephalus*. E. *Barilius bola*. Dorsal views.

then becomes perpendicular to form a broad shaft. The upper lateral face bears a well-developed flange across which passes the *dilatator operculi* muscle and from which part of *adductor mandibulae* A_2 originates. The posterior border of the hyomandibula overlaps the dorsal part of the preoperculum and its medial face is almost flat and produced dorso-posteriorly as a compressed condyle with which the operculum articulates.

The *metapterygoid* has a markedly concave dorsal border, the posterior part of which is formed into a wide triangular process directed somewhat anteriorly. This process is a point of attachment for the *levator arcus palatini* muscle. The ventral border is concave and forms the dorsal margin of a large fenestra. Posteriorly the metapterygoid extends to overlap the lower limb of the hyomandibula.

The *symplecic* is a long curved bone forming part of the ventral border of the fenestra. It is separated by cartilage from both the lower limb of the hyomandibula and the metapterygoid.

The *quadrate* has a long ventral border overlapping the symplectic. The lateral face of this part of the bone projects as a wide shelf and provides a surface for the origin of the *adductor mandibulae* A_1 muscle. The ascending face of the quadrate is axe-shaped, its concave inner border forming the anterior margin of the fenestra, its outer border is curved slightly backwards.

The *entopterygoid* has a slightly convex dorsal border and is directed medially to contact the parasphenoid. It underlies the medial faces of both the metapterygoid and quadrate.

The *ectopterygoid* is a narrow lamellate bone with a convex border. It articulates with a narrow ledge along the border of the metapterygoid.

The *palatine* is triangular in cross-section, its ventral border produced into a lamellate edge. The bone narrows anteriorly to form into an articular head bearing a lateral process and a medial facet which abuts against the preethmoid cartilage. Posteriorly the palatine fits into a right-angled excavation in the border of the entopterygoid; a ligament joins its ventral edge to the ectopterygoid (see Fig. 38A in Howes, 1978).

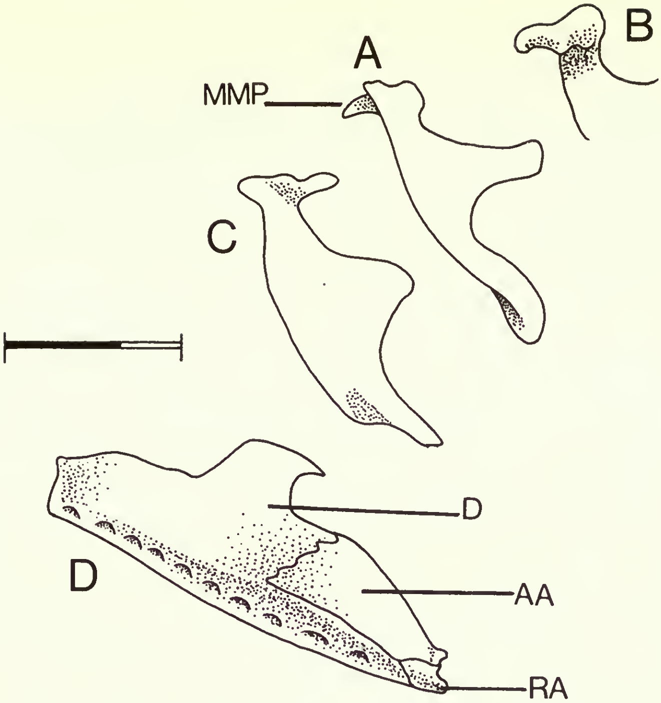


Fig. 33 *Engraulicypris sardella*, upper and lower jaws. A. Maxilla (lateral view). B. Maxillary process (medial view). C. Premaxilla (lateral view). C. Dentary (lateral view).

Zacco

The *hyomandibula* differs from that of *Opsariichthys* in that there is no separation of the anterior and posterior facets; the entire dorsal border being a condylar surface. The anterior dorsal edge slopes forward at a more oblique angle, the upper part of the bone is narrower and has an almost perpendicular anterior margin and the lateral flange is absent.

Zacco pachycephalus differs from other species in that the hyomandibula bears a well-developed lateral flange (see p. 189).

Other features in which the hyopalatine arch of *Zacco* differs from that of *Opsariichthys* are the lack of a metapterygoid process (except in *Z. pachycephalus*; see p. 189), a smaller metapterygoid – quadrate fenestra (the correlate of a wider quadrate and a deeper metapterygoid) and the absence of a ventral lamellate ridge on the palatine.

Luciosoma

The *hyomandibula* closely resembles that of *Opsariichthys* in having a long dorsal border, shallowly separated articular facets and well-developed lateral flange. The *quadrate* lacks the lateral shelf present in *Opsariichthys*. The *metapterygoid* process is absent and the metapterygoid–quadrate fenestra, although present, is very small. The ventral border of the *entopterygoid* is longer than in *Opsariichthys* and there is a corresponding lengthening of the *ectopterygoid*. The *palatine* bears a rounded ventral ridge.

Barilius

Group A. There is some interspecific variation in the morphology of the hyopalatine arch, viz.: the *hyomandibula* bears separate condyles, although the degree of separation is variable, as is the development of the lateral flange. The *metapterygoid* dorsal process is absent in all species but in *B. bendelisis* the dorsal border is markedly concave and shaped into a long posterior process. A metapterygoid–quadrate fenestra is sometimes lacking.

Group B. The anterior and posterior condyles of the *hyomandibula* are widely separated, the anterior extending forward at an angle of 45° to the vertical to articulate in a small sphenotic–pterosphenoid fossa; the posterior condyle is high, its narrow dorsal surface articulating with the long pterotic fossa. The lateral face of the hyomandibula bears a long, laterally extending flange which, in *B. bola*, is curved upwards so as to form a deep cavity. The anterior hyomandibula border is concave.

The *metapterygoid* in all species bears a long anteriorly directed dorsal process. This process is in the form of a gutter with the open side being dorsad. It provides both an insertion channel for fibres of the *levator arcus palatini* muscle and as a point of origin for fibres of the *adductor mandibulae* A_3 muscle. This process is developed to the greatest extent in *Barilius bola* and *B. guttatus*, its distal tip almost reaching the same horizontal plane as the top of the anterior hyomandibular condyle. The posterior border of the metapterygoid extends more than halfway along the lateral surface of the hyomandibular stem (see Fig. 38B in Howes, 1978).

The *symplectic* is well developed and deep; the *quadrate* is also deep with a laterally produced ventral border as in *Opsariichthys*. The *ectopterygoid* is very elongate with a strongly concave lower margin. As in *Opsariichthys* the *palatine* bears a strong ventral ridge. A metapterygoid–quadrate fenestra is absent.

Group C. As in *Group B* the *hyomandibular* condyles are widely separated but the anterior condyle is much thicker than in any of those species and in this respect more closely resembles the *Opsariichthys* condition. The lateral flange is weakly developed and the anterior border irregularly concave. The *metapterygoid* bears a small posterior lamellate process similar to that in *Opsariichthys*. The *quadrate* is shallow, its ventro-lateral border well produced; the *symplectic* elongate and the *palatine* with a well-developed, knife-edged ventral ridge. There is no metapterygoid–quadrate fenestra.

Engraulicypris

The *hyomandibula* has a long upper face, with an almost continuous articulatory dorsal border and a convex anterior margin. The dorsal posterior edge is extended to form a triangular condyle. The *metapterygoid* is directed medially at a sharp angle so as to form an almost flat shelf. The medial part of the bone is produced into a long lamellar process. The *quadrate* is deep, its ventral posterior border produced into a thin spine. The *palatine* bears a slight lateral process which is separated from a medial process by a deep channel. A ligament joins the lateral process to the antero-dorsal part of the maxilla (LPM, Fig. 34). Another ligament (LPE) joins the palatine shaft to the ethmoid, and a further one (LPEK), which passes over the ethmoid arm, attaches the medial palatine process to the kinethmoid shaft.

Opercular series

Opsariichthys

The *operculum* is deep with a short dorsal border, the dorso-anterior process is curved outwards. The articulatory facet for the hyomandibular condyle is situated dorso-medially; extending posteriorly from the facet is a thin strut pierced by two foramina. The *preoperculum* bears four latero-sensory canal pores along its nearly vertical upright limb and three along the horizontal part. The *suboperculum* has a well-rounded ventral border and dorsally is partially covered by the operculum. The *interoperculum* is wide and is largely covered by the preoperculum laterally.

Zacco

There is little difference between *Zacco* and *Opsariichthys*, except that the anterior dorsal process of the operculum is feebly developed.

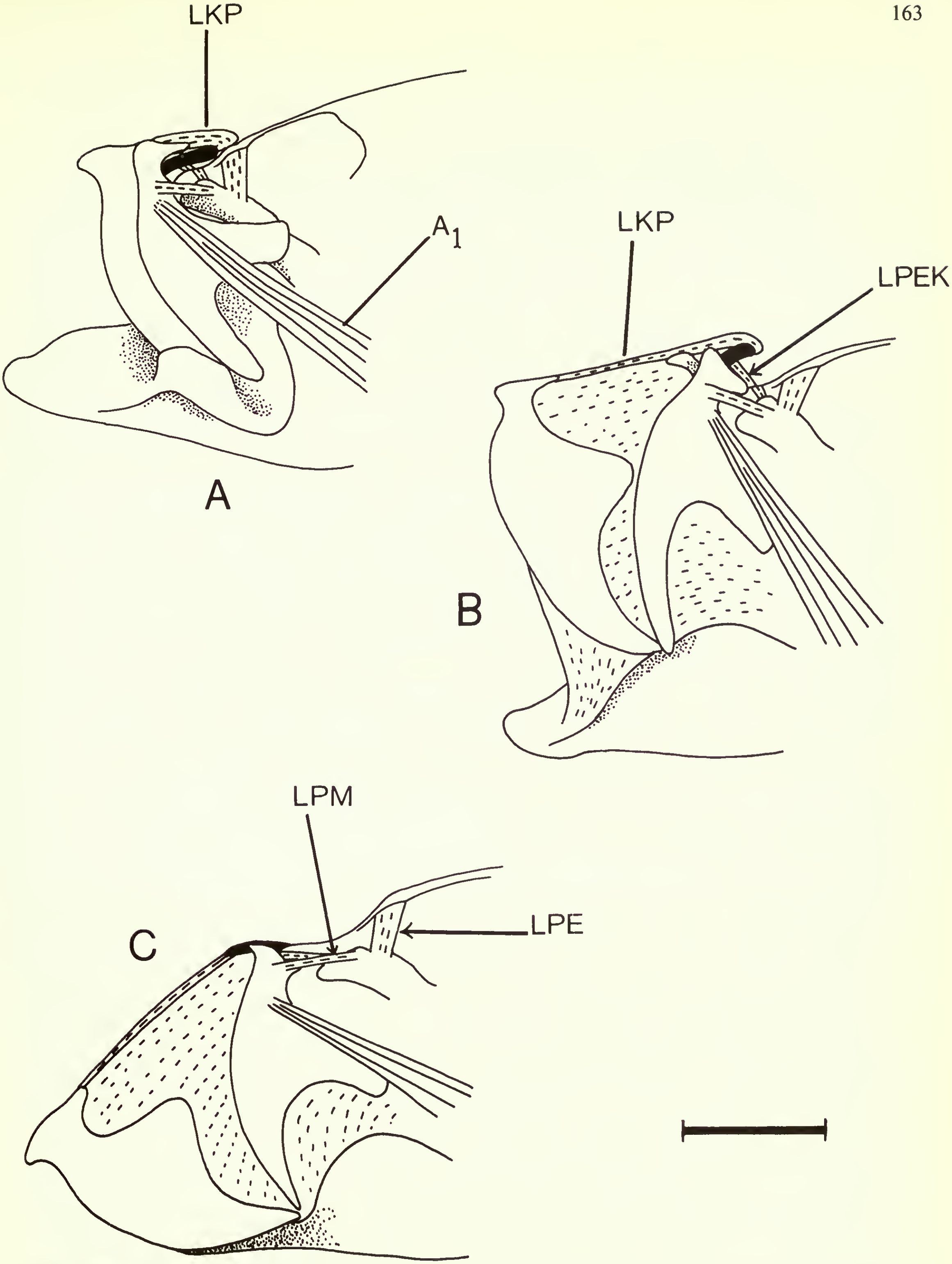

LKP
A1
A
LKP
LPEK
B
LPM
LPE
C

Fig. 34 *Engraulicypris sardella*, sequence of jaw protrusion (semi-diagrammatic). A. 1st stage, mouth partially open. B. Intermediate stage, mouth completely open. C. Final stage, upper jaw fully extended

Luciosoma

The upright limb of the *preoperculum* is aligned at 45° to the vertical, and its horizontal limb is short. The *operculum* has a well-rounded border and is much shallower than in either *Opsariichthys* or *Zacco*; its anterior dorsal process is feebly developed.

Barilius

Group A. The opercular series differs little from that of *Opsariichthys* or *Zacco*, but in the species of *Group B* the upright part of the preoperculum is inclined at an angle of 30° to the vertical and the horizontal limb is short. In *Barilius loati*, *steindachneri* and *kingsleyae* the width of the *operculum* is greater and the anterior dorsal process more highly developed and anteriorly extended than in any other species of the group. In *Group C* the opercular border is slightly concave and its lower posterior border produced.

Engraulicypris

The *operculum* has a long, straight dorsal border and its posterior margin is only slightly convex.

Comments on the jaws, hyopalatine and opercular series

In a previous paper (Howes, 1978) I made some comment on the jaw bones of various cyprinids and considered those of *Opsariichthys* as relatively primitive. However, I now realize that in some respects they are highly specialized and that the separation of the premaxilla and maxilla, and the strongly developed symphysial knob and notch must be considered as derived features. Only in *Macrochirichthys* is there a similar development of the symphysial knob, but this is regarded as a parallelism; Howes (1979). The coronoid process of all the genera under consideration is of the plesiomorph form, i.e. relatively high and without any contribution from the anguloarticular bone (Howes, 1978).

There is some variation in the degree of development of the anterior ascending premaxillary processes in the taxa under discussion. In *Opsariichthys*, *Zacco* and *Barilius Group A*, the ascending processes are long, with concave lateral borders and rounded dorsal tips. In *Luciosoma* the processes are shorter with broader tips and in *Barilius Group B* the processes are much reduced with a completely convex lateral border. Although in *Barilius Group C*, the lateral border of the premaxillary process is concave the dorsal tip is triangular, allowing for closer contact with the expanded kinethmoid (Fig. 32). Likewise, a transformation series can be seen in the development of the anterior part of the maxilla where in *Barilius Group A*, the tips of each maxilla are widely separated from each other but become progressively more elongate in *Opsariichthys* and *Luciosoma* until, in *Barilius Groups B* and *C*, they almost contact each other across the midline.

The curved walls of the dentary are shared features of *Opsariichthys* and *Luciosoma*; the anterior medial maxillary processes make direct contact along the midline in all genera except *Zacco* where contact is indirect and *via* a ligament; this is the condition usually encountered in the Cyprinidae and is therefore considered to be the plesiomorph one.

Engraulicypris sardella differs from all other genera reviewed here in the marked development of highly protrusile jaws. The high degree of protrusibility is attained by the prolongation of the ethmoid arms in conjunction with ventrally directed maxillary processes which enables the kinethmoid to rotate through more than 180°. The ligament connecting the distal tip of the kinethmoid to the anterior border of the premaxilla is extremely long and when the jaws open and protrude, the tensed ligament extends almost horizontally. When the jaws close and retract, the kinethmoid pivots (in the anterior vomer notch, see p. 137) so that it again lies horizontally between the ethmoid arms. The long ligament curls over and folds into the ethmoid indentation (Figs 34A–C). The ventrally directed medial maxillary process is a feature shared with *Leptocypris* (see p. 181).

The most significant features of the hyopalatine series concern the hyomandibula and the metapterygoid. Only in *Zacco* and *Engraulicypris* does the *hyomandibula* lack the marked separation of its articular condyles. The most extreme separation is found in *Barilius Group B*. It could be argued that such a separation of the condyles is a correlate of the elongation of the head. Admittedly this is partly so, for in *Barilius Group B* there is some lengthening of the otic region. However, in other cyprinids (such as the aspinines) where there has been considerable elongation of the skull (see Howes, 1978) there is no correspondingly great separation of the hyomandibular condyles. Neither have I found such a feature in piscivorous long-headed characins. The significance of the bipartite hyomandibula in functional terms is probably to be explained by the vertical elongation of the suspensorium rather than through the horizontal elongation of the skull. Whether or not this is so, the feature is certainly a derived one and is synapomorphous for *Opsariichthys*, *Barilius* and *Luciosoma*. In these genera the *hyomandibula* also bears a lateral flange, which again is developed to the most marked degree in *Barilius Group B*. Although a character occurring in other cyprinids (see Howes, 1978 and comments by Forey, 1975) it is here identified as a synapomorphy.

The metapterygoid in *Opsariichthys* and *Barilius Groups B* and *C* bears a dorsal posterior process. An incipient condition of this process is present in *Opsariichthys* and *Barilius Group C*, whilst an increasing grade of development is manifest throughout *Group B*, as is also a deepening of the metapterygoid. I have failed to find such a feature in any other group of cyprinids and therefore regard this as a synapomorph character linking those genera in which it occurs.

Engraulicypris sardella differs from the other genera both in the form of the hyomandibula and the metapterygoid. Although there is no marked separation of the hyomandibular condyles, the posterior condyle is produced into a triangular shape which articulates with a fossa on the posterior border of the pterotic. In this taxon, unlike *Zacco*, it is probably a derived feature, the form of the articulation suggesting a wide lateral movement of the hyomandibula. The metapterygoid spine in *Engraulicypris* also differs from that in *Barilius Groups B* and *C* in that it originates from the anterior part of the metapterygoid and serves as a site of attachment for the *adductor arcus palatini* instead of the *levator arcus palatini* as in the other taxa. A deep lateral shelf along the ventral part of the quadrate is also shared by *Opsariichthys* and *Barilius B* and *C*.

The metapterygoid–quadrate fenestra has been discussed at some length in an earlier paper (Howes, 1978). It need only be mentioned that of those genera discussed here it is present in *Opsariichthys*, *Zacco* and *Luciosoma;* its occurrence in other groups of cyprinids (Howes, 1979) suggests that it is a plesiomorph feature.

The elongate *symplectic* found in *Opsariichthys*, *Zacco*, *Barilius Groups A* and *C* and in *Luciosoma* is the 'usual' cyprinid condition and is thus considered to be plesiomorphic. The short, deep symplectic in *Barilius B* is a derived feature.

The *opercular series* differs little between the genera; only in *Luciosoma* and *Engraulicypris* is there any marked elongation of the operculum and shortening of the preoperculum, whilst in *Engraulicypris* the interoperculum is finely serrated.

Hyoid and branchial arches

Opsariichthys

There are few features distinguishing these elements from those of other cyprinids (Ramaswami, 1955; Howes, 1978). Attention is drawn to the narrow waisted ceratohyal, reduced ventral hypohyal and the three broad branchiostegal rays. The basihyals are all short.

Each *ceratobranchial* bears 8–9 gill rakers. The pharyngeal bone bears three rows of curved teeth (dental formula, 2.3.5). The 4th *epibranchial* has a broad, triangular dorso-medial process posteriorly and a short, rod-like process midway along its length (Fig. 35). There are two ossified *infrapharyngobranchials* identified as the 2nd and 3rd. The 3rd is an extensive triangular element spanning the medial surfaces of epibranchials 3 and 4. A cartilaginous element at the outer edge of infrapharyngobranchial 3 and articulating with the 4th epibranchial probably represents the 4th infrapharyngobranchial.

Chu (1935) studied the pharyngeal bones of *Opsariichthys* and *Zacco* and noted that those of the former genus were narrow and elongate, whilst those of the latter were short and broad. A similar distinction can be found within the groups of *Barilius*, those of *Group A* resembling *Zacco*, with *Groups B* and *C* and *Luciosoma* resembling *Opsariichthys*.

In *Engraulicypris sardella* the *ceratobranchials* are very long and bear 24–25 long, slender gill-rakers. The pharyngeal bone has 3 rows of compressed teeth (dental formula: 5.3.2) with finely serrated cutting edges and recurved tips.

Pectoral girdle (nomenclature follows that of Brousseau, 1976)

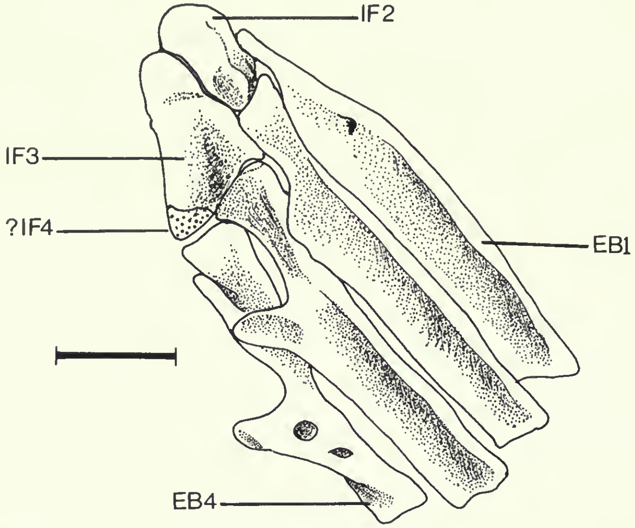


Fig. 35 *Opsariichthys*. Upper branchial arches, dorsal view.

Opsariichthys

The upright part of the *cleithrum* is perpendicular and bears a well-defined ridge along its anterior border (Fig. 36A). This ridge broadens ventrally and fans out to form a broad, horizontal cleithral lamina; the leading edge of the horizontal limb is rounded. There is a well-developed ventro-medial cleithral ridge. The posterior cleithral lamina is broad with a straight border. The anterior fenestra is well developed. The *supracleithrum* is very elongate. Each *coracoid* is small and when viewed laterally is seen to extend only slightly below the ventral margin of the cleithrum. The coracoids diverge, meeting only anteriorly; the *mesocoracoid* shaft is long, rounded and perpendicular. The *postcleithrum* is short and spatulate, curves mesially with its ventral tip on a line level with the ventral border of the coracoid (Fig. 36B). There are four proximal *radials*, the 3rd and 4th being lamellar.

Zacco

The pectoral girdle morphology is basically that of *Opsariichthys* but the sternohyoid ridge on the cleithrum is greatly produced anteriorly resembling that in *Danio* (see Howes, 1979). The *supracleithrum* is short and its anterior edge straight with a slight distal notch. The *postcleithrum* is shorter than in *Opsariichthys* and its ventral tip pointed instead of spatulate.

Luciosoma

The upright part of the *cleithrum* is shorter than in *Opsariichthys* or *Zacco* and the posterior lamina is extended (Fig. 37A). The horizontal limb is broad with a moderately developed ridge.

The *supracleithrum* is short, the *coracoids* shallow, meeting each other along the midline and containing a large anterior fenestra. The most outstanding feature of the pectoral girdle is the form of the postcleithrum. It is a broad lanceolate bone attached to the edge of the posterior cleithral lamina extending laterad to the body scales. Its tip is enclosed in a fleshy sheath and this sheath extends as the pectoral axial lobe (see Fig. 37A & p. 168) to lie between the pectoral fin and the body. There are no tendons attached to the postcleithrum.

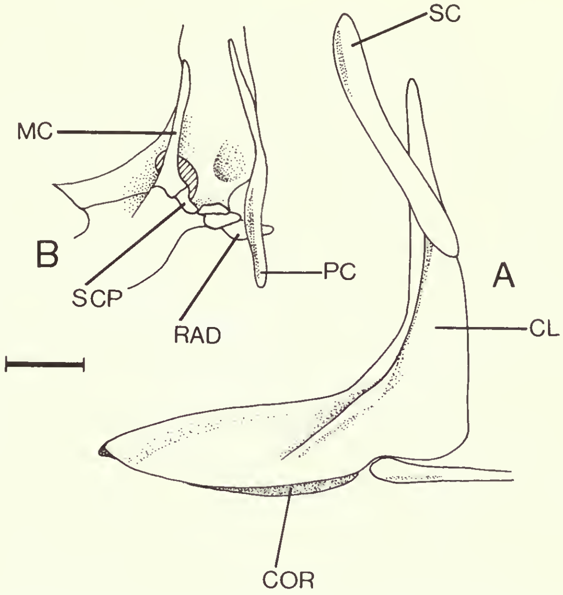


Fig. 36 *Opsariichthys*. Pectoral girdle in A, lateral and B, medial views.

Barilius

Within *Group A* there is some variation in the morphology of the pectoral girdle; the upright part of the *cleithrum* is generally short with a posteriorly extended lamina; the *supracleithrum* is elongate, the *coracoids* variable in depth but never joining along their medial faces.

In *Group B* the upright part of the *cleithrum* is very narrow with a well-developed anterior ridge, and the *supracleithrum* is long and narrow (Fig. 37B). The *coracoids* are very shallow and meet anteriorly along their ventral margins; the *mesocoracoid* shaft is broad and lamellar. The development of the anterior fenestra is variable, being small in *B. loati* and extensive in *B. bola*.

Species of *Group C* possess a broadly lamellate upright cleithral limb with an expanded posterior edge to which is attached a spatulate postcleithrum. The *supracleithrum* has only a slight anterior inclination as compared with other *Barilius* where it is inclined at 45° to the cleithrum. The coracoid is well developed, with a curved ventral margin and a large anterior fenestra. The mesocoracoid shaft is broad and lamellar.

In all *Barilius* species examined the *postcleithra* are small and spike-like, medially directed bones which unlike the postcleithrum in *Luciosoma* do not support an axial flap or scale.

Engraulicypris

The upright part of the *cleithrum* is short, its ventro-posterior edge extended backwards as a long spine. The *coracoids* are shallow and meet each other along the midline. A *postcleithrum* is absent.

Comparisons

The most notable variations in the pectoral girdle are in the vertical and horizontal extensions

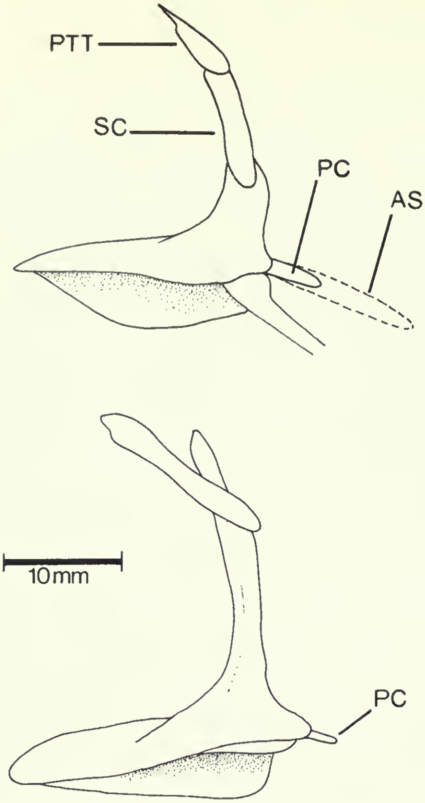


Fig. 37 Pectoral girdles of A, *Luciosoma bleekeri*, B, *Barilius bola*.

of the cleithrum. It has been noted previously (Howes, 1978) that in some long-jawed cyprinids such as *Barilius bola* the vertical limb is long and narrow. In *Luciosoma*, on the other hand, as in the aspinines (Howes, 1978), the upper limb is short and broad and more closely resembles that in *Opsariichthys*. The postcleithrum in *Opsariichthys* and *Zacco* is elongate and medially directed as, indeed, it is in the majority of cyprinids examined – and this is taken to represent the plesiomorph condition. In all *Barilius* species it is reduced to a spike-like or scale-like bone and in *Luciosoma* lies horizontally above the axial aperture and supports the axial lobe. The only other cyprinids in which the postcleithrum supports the axial lobe is a group of *Rasbora* species (represented by *R. argyrotaenia*); however, here the postcleithrum is thin and ventrally directed. In the cheline *Securicula* the postcleithrum is absent and 'replaced' by a large scale covering the dorsal border of the axial aperture. In chelines a reduction of the postcleithrum was considered a derived character but some forms of postcleithral elongation, as in the case of *Macrochirichthys*, could also be interpreted as derived (Howes, 1979). In the case of the bariliines I regard reduction of this element as an apomorphy, likewise in *Engraulicypris* where it is absent.

Vertebral skeleton

Opsariichthys

Weberian apparatus (Fig. 38). The 1st vertebra bears strong lateral processes which are rounded proximally and compressed distally. The 2nd vertebra has a thick lateral process which is inclined upward. The 2nd and 3rd vertebrae are not fused together and the 3rd bears a wide fossa on its postero-lateral face for the articulation of the tripus. The 3rd vertebra is expanded dorsally into the 3rd neural plate which extends laterally and curves forward along the top of the 2nd centrum. The anterior border of the 3rd neural plate slopes downward and is joined to the 2nd neural plate. The neural complex is steeply raised, its curved dorsal border being deeply grooved; the anterior border is rounded and extends forward to above the 2nd neural plate. The ossicles differ little from those of other cyprinids (Ramaswami, 1955; Howes, 1978) except that the tripus is much elongated, its posterior tip extending to below the 6th centrum.

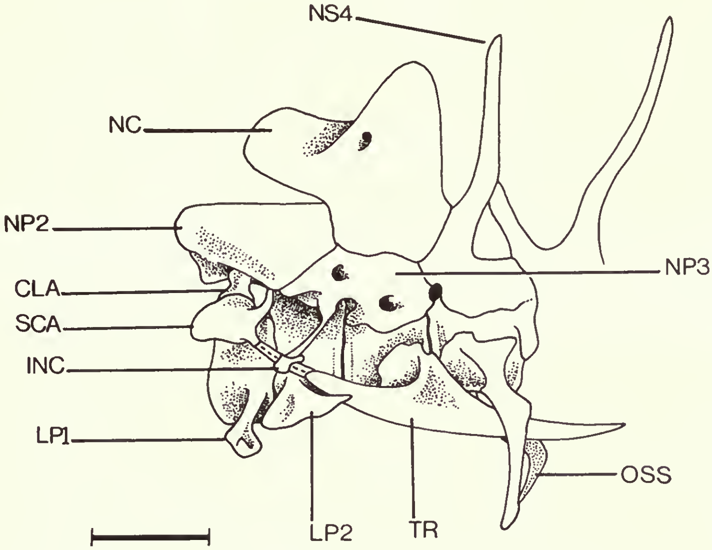


Fig. 38 *Opsariichthys* Weberian apparatus, lateral view.

Vertebral column
There are 44 vertebrae (21 abdominal, including the 4 comprising the Weberian apparatus + 22 caudal + the fused pre-ural and 1st ural vertebra – counted as a single element in Table 1) and 6–7 supraneurals, the first being an irregularly shaped lamellate element, the others lanceolate.

Caudal fin skeleton (Fig. 39). There are 6 hypurals, none of which are greatly expanded, the 6th being a small element. The fused pre-ural and ural centrum (PU1 + U1) bears a blunt neural spine. There is one epural and a pair of slender uroneurals lying above hypural 6. The parhypural bears a well-developed broad hypurapophysis.

Comparisons
The intergeneric differences in the morphology of the vertebral column are those involving the anterior vertebrae which form the *Weberian apparatus*.

In *Zacco* the lateral processes of the 1st vertebra are reduced, whilst those of the 2nd are greatly extended. This is similar to the condition in *Opsariichthys*, and likewise the 2nd and 3rd vertebrae are separate.

In *Barilius Group A* the 1st and 2nd vertebrae are of the type encountered in *Opsariichthys* and *Zacco* but the 2nd and 3rd centra are fused. The lateral processes of the 1st vertebra in *Barilius Group B* are short and those of the 2nd are elongate with pointed tips and are directed posteriorly at 45° to the transverse plane. In *Barilius Group C* the processes of the 1st vertebra are curved backwards and partly underlie those of the 2nd vertebra. The lateral processes of the 2nd are long with rounded tips and extend horizontally. The 2nd and 3rd vertebrae of all *Barilius* species examined are fused together.

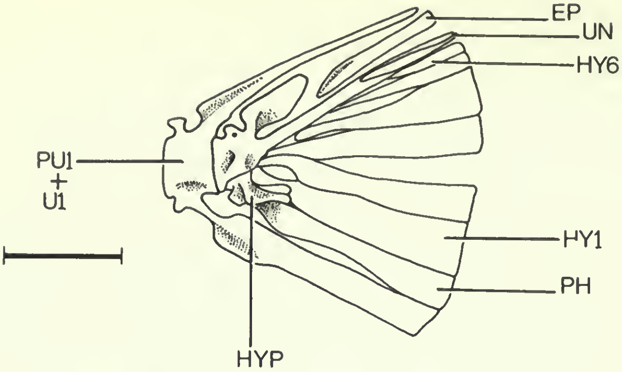


Fig. 39 *Opsariichthys* Caudal fin skeleton.

Engraulicypris has short lateral processes on the 1st vertebra and long, posteriorly directed ones on the 2nd (similar to *Opsariichthys*). *Luciosoma*, on the other hand, has long 1st vertebral processes and expansive, wing-like processes on the 2nd vertebra (Fig. 40), a feature shared with some species of *Rasbora* (p. 182).

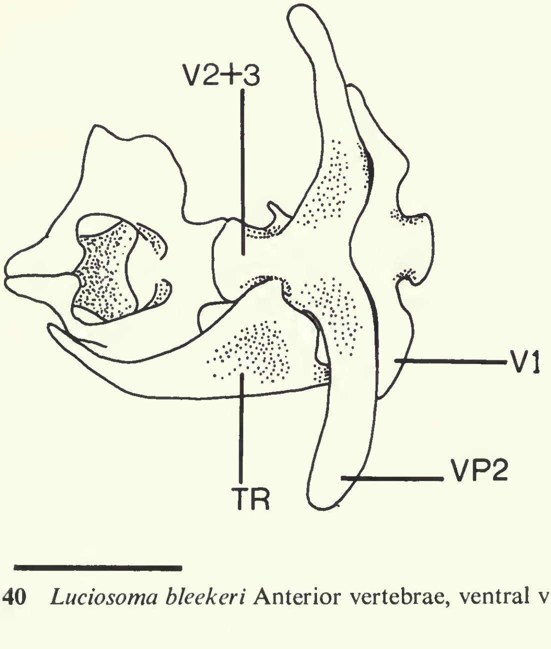


Fig. 40 *Luciosoma bleekeri* Anterior vertebrae, ventral view.

The morphology of the 1st and 2nd vertebrae exemplified by *Opsariichthys* appears to be widespread amongst the cyprinids and is taken to represent the plesiomorph condition. The long, sharply caudally directed 2nd vertebral processes of *Raiamas* and the expanded type of *Luciosoma* are considered apomorphies.

One feature that seems common to all genera studied here is the form of the *ossa suspensoria*. These bones are obliquely angled backwards so that their tips come to lie below the centre or posterior part of the 5th centrum. Also, the lateral extension of the os suspensorium (4th pleural rib of Ramaswami, 1955) is short and directed somewhat anteriorly. Only in *Zacco* are the ossa suspensoria long and vertically directed, their tips meeting below the 4th centrum. This latter condition is widespread amongst the cyprinids and is therefore reckoned as being the plesiomorph one.

Previously (Howes, 1978) I had given the caudal fin ray count in cyprinids as I9+9I. This is an error, I have now examined radiographs of many cyprinid genera and am in agreement with Roberts (1973) that the count is I9+8I.

Table 1 The modal number of vertebrae of various species used in this study

	Opsariichthys uncirostris	44	(4+17+22+1)
	Zacco temmincki	43	(4+18+20+1)
	Zacco pachycephalus	40	(4+17+18+1)
	Zacco platypus	40	(4+17+18+1)
	Zacco macrophthalmus	42	(4+17+20+1)
	Zacco barbatus	42	(4+18+19+1)
	Luciosoma setigerum	43	(4+21+17+1)
	Luciosoma bleekeri	42	(4+21+16+1)
	Luciosoma trinema	39	(4+18+16+1)
	Luciosoma spilopleura	40	(4+18+17+1)
	Rasbora argyrotaenia	34	(4+12+17+1)
	Rasbora elanga	42	(4+17+20+1)
Group A	*Barilius barila*	40	(4+15+20+1)
	Barilius tilheo	42	(4+16+21+1)
	Barilius ornatus	41	(4+16+20+1)
Group B	*Barilius bola*	47	(4+20+22+1)
	Barilius guttatus	47	(4+18+24+1)
	Barilius lujae	41	(4+16+20+1)
	Barilius salmolucius	43	(4+16+22+1)
	Barilius macrostoma	44	(4+17+22+1)
	Barilius kingsleyae	41	(4+15+21+1)
	Barilius loati	44	(4+17+22+1)
	Barilius moori	43	(4+15+23+1)
	Barilius microlepis	47	(4+17+25+1)
Group C	*Barilius ubangensis*	43	(4+16+22+1)
	Barilius microcephalus	45	(4+16+24+1)
	Leptocypris modestus	40	(4+15+20+1)
	Barilius niloticus	37	(4+14+18+1)
	Engraulicypris sardella	44	(4+19+20+1)

Note: Those species in which there is a high number of vertebrae are either very elongate fish (*B. bola, B. guttatus*) or lacustrine species (*B. microlepis*).

External anatomical features

Tubercles

Opsariichthys

Keratinized tubercles are present on the head and sometimes on the scales of the flanks and anal fin rays of all species. They are present in both sexes but are most prominently developed on males with ripe testes. The arrangement of the tubercles on the head is shown in Fig. 41A and is: 1st infraorbital, 2 or 3 on the dorsal border, 2 on the ventral; 2nd infraorbital 5; 3rd infraorbital 5 or 6; 4th absent; 5th absent; preoperculum, 5 or 6 along the lower border; premaxilla (upper lip) 5–8; dentary, 3 rows, 8 dorsal, 12 middle, and 8 ventral; nasal 2–3 situated lateral to the nasal bone; supraorbital 4–5; cheek, 10–12, small and irregularly scattered.

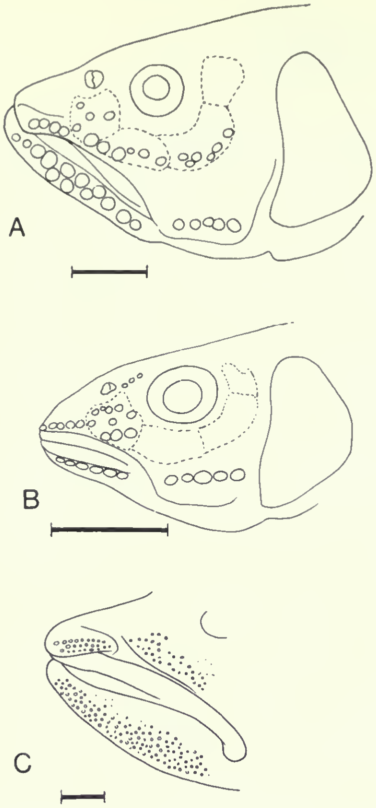


Fig. 41 Arrangement of tubercles on the heads of A. *Opsariichthys uncirostris*. B. *Zacco macrophthalmus*. C. Tubercle arrangement on the jaws of *Barilius microlepis*. Scales = 5 mm.

The tubercles are conical but are inclined so that on the anterior part of the lower jaw and the 1st infraorbital the cones point caudad; on the 2nd and 3rd infraorbitals they are perpendicular whereas on the posterior part of the cheek they incline forward. The tubercles are attached to the skin through thickened pads of tissue and when a tubercle is removed there remains a circular pit bearing lamellar radii. In specimens where the tubercles have been shed in life, there remains a shallow, saucer-shaped depression.

Zacco

The tubercles are of the same conical form as in *Opsariichthys* and are present on the snout, 1st infraorbital, nasal, cheek below the infraorbitals, lower jaw, preoperculum and operculum (Fig. 41B). They are also well developed on the anal fin rays and on the scales both below and above the lateral line. Bănărescu (1968) described the tubercle distribution in the various species of this genus.

Luciosoma

No tubercles have been found in any species examined. The skin covering the ethmoid region is deeply grooved by two or three S-shaped channels which extend from the nasal opening to the midline (see p. 175).

Barilius

Tubercles are present in many species of *Barilius* of all three groups. In *Groups A* and *B* they are small and in many species appear to be present only on the head. In *Barilius gatensis* the tubercles of the lower jaw extend onto its medial surface (Fig. 42). In a specimen of *B. ansorgii* (*Group B*) tubercles are distributed over most of the dorsal and lateral parts of the body. In ripe males of *Barilius microlepis* (*Group C*) of Lake Malawi, the area covering the tip of the upper jaw, the infraorbitals and the entire lower jaw are covered with minute tubercles giving the jaws a granular appearance (Fig. 41C). In these specimens tubercles are also present on the anal fin rays. In other species of this group (*B. ubangensis* and *B. zambesensis*) the tubercles are well developed and in their pattern resemble those of *Opsariichthys*.

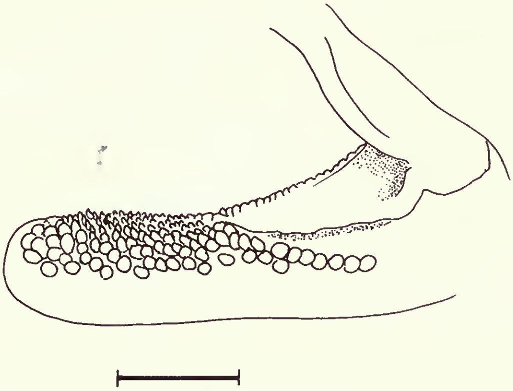


Fig. 42 *Barilius gatensis*. Tubercle arrangement on the left lower jaw.

Engraulicypris

No tubercles have been found in *Engraulicypris sardella*.

Pectoral and pelvic lobes

Opsariichthys

An axial pectoral lobe is present in the form of a minute fleshy appendage. There is also a fleshy triangular lobe lying medial to each pelvic fin.

Zacco

There is some intraspecific variability in the form of the pectoral and pelvic lobes. In *Z. platypus* the pectoral lobe is very small and the pelvic lobe is in the form of a scale with a fleshy border. In *Z. temmincki* the pectoral lobe is well developed and the pelvic scale has a fleshy border. In *Z. macrophthalmus* the pectoral lobe is barely developed and the pelvic one is an elongate scale without a fleshy margin. In *Z. pachycephalus* the pectoral lobe is bipartite and the pelvic lobe a thick fleshy wedge (see p. 189).

Luciosoma

The pectoral axial lobe is an elongate, ventrally curved structure originating from the post-cleithrum (see p. 167). An elongate pelvic scale is also present.

Barilius

The pectoral and pelvic lobes are developed as fleshy structures only in *Group C*. This is particularly so in *B. ubangensis* and *B. microlepis*. In the latter species the pectoral lobe in males is expanded and in a specimen of 430 mm SL the lobe is a complexly divided structure (Fig. 43); in females it is reduced and scale-like.

In *Barilius Group A* a pectoral scale with a wide fleshy border is developed, and in *Group B* the scale is elongate without such a border.

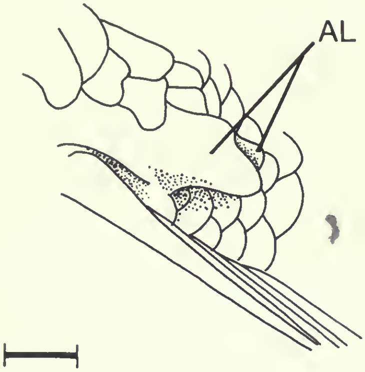


Fig. 43 *Barilius microlepis.* Axial pectoral fin lobe of a specimen 430 mm SL.

Engraulicypris

Pectoral lobes are absent, but an elongate pelvic scale is present.

Anal fin

In *Opsariichthys* and *Zacco* the 3rd, 4th and 5th anal fin rays in both sexes are extended, particularly so in males. The tips of the rays are expanded and separate into 9–10 branches. The posterior ventral surface of the caudal peduncle in both genera is somewhat fleshy and particularly in *Zacco* becomes ventrally extended into a keel. This keel forms an uninterrupted margin to the ventral aspect of the body when the long anal fin is folded and presumably aids in streamlining (Figs 44A & B).

The anal fin is not extended in males of *Luciosoma* species, although in some individuals a filament is developed from the first ray.

In *Barilius Group C* there is an extension of the first four to six rays in males. This is particularly evident in *B. ubangensis* which also displays a colour pattern of the dorsal fin remarkably similar to that of *Zacco*. The anal fin is not extended in other groups of *Barilius*.

Comments on tubercles, axial lobes and fins

The tubercles, axial lobes and anal fin are considered together because their development appears to be correlated. A series of well-developed tubercles on the head, body and anal fins is associated with marked secondary sexual dimorphism exhibited by the attenuation of the anal fin in the males, by fleshy pectoral axial and pelvic lobes and distinctively marked dorsal and anal fins in both sexes. Such a combination of features is shared by *Opsariichthys*, *Zacco* and *Barilius Group C*.

It seems likely that these characters are associated in a reproductive context. It has been assumed that tubercles play some part in reproductive behaviour, possibly functioning as stimulatory tactile organs (see Wiley & Collette, 1970). In this regard Nakamura (1969) states that in *Zacco* the male makes use of the tubercles to drive away intruders and rival males from its territory. It must be said that it is not clear from the English translation of this passage whether Nakamura has actually observed this behaviour or conjectures it. Okada (1960) notes that in *Zacco* the male ' . . . moves quickly against rocks' cleaning areas for the deposition of the eggs. He goes on to say ' . . . In this connection, it is interesting to note that the pearl organs of Japanese Cyprinoid fishes develop mostly about the tip of the snout and on the side of the face'. Presumably the connection implied, but not stated, is that the tubercles in some way either aid in cleaning the

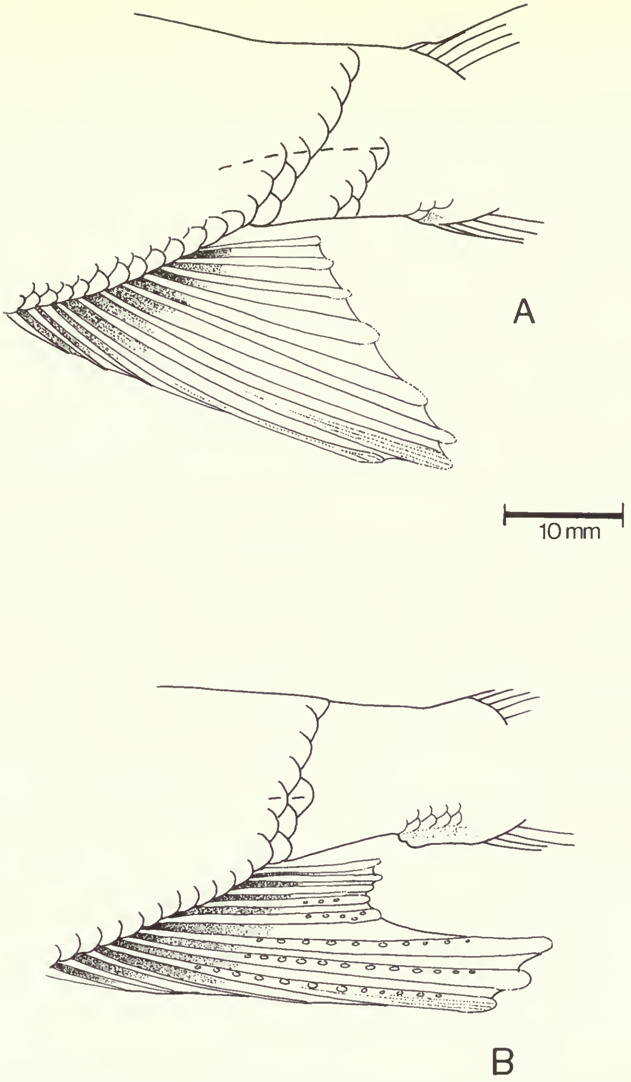


Fig. 44 Anal fins of A, *Opsariichthys uncirostris bidens* (BMNH 1901.3.6 : 6) and B. *Zacco platypus* (BMNH 1969.4.15 : 29–31).

rock surfaces or act as a buffer. But then Okada proposes that '. . . The tubercles probably serve as contact organs, holding the mating pairs entangled by increasing the roughness of the surfaces of the body of the male which come into contact with the body of the female'. I cannot see how the second statement is linked with the first, and there are no published first-hand observations to justify it.

In contrast to the idea that tubercles act as contact organs, Reid (unpublished thesis and pers. comm.) has hypothesized that at least in *Labeo* their presence is more likely to serve some hydrodynamic function but one nevertheless correlated with reproductive activity in as much as these fishes move upstream to spawn, thus encountering a particular kind of water turbulence. This is likely to be the case in *Opsariichthys*, *Zacco* and some *Barilius*. The orientation of the tubercles on the head of *Opsariichthys* and *Zacco* (see above, p. 172) suggest a hydro-mechanical function. A similar function may be attributed to the transverse grooves on the snout of *Luciosoma*

(p. 172) which possibly serve to counteract turbulence in that region by improving streamlining (Reid, pers. comm.).

A fleshy axial pectoral fin lobe is not confined only to the genera considered here, but is also present in the American cyprinid, *Platygobio*, some cultrines, alburnines and some species of *Rasbora*. In *Platygobio* it is a small structure not attached to the cleithrum. In the *Rasbora* species it is large, usually elongate and attached to the postcleithrum as in *Luciosoma*. In the cultrines and alburnines the lobe can be small or elongate, ventrally curved and is attached to the cleithral lamina. No data are available on the possible use of this organ. It is possibly associated with reproductive behaviour and could act as (i) a visual stimulant when the male extends his pectoral fins, and/or (ii) a tactile organ if the female curves her body around that of the male and/or (iii) as an area in which pheromone-producing cells are concentrated.

Another character, possibly correlated with the development of the anal fin and axial lobes, is the presence of 'pectoral pads' in some species of *Barilius*. These pads were first mentioned by Hora (1921) in *Barilius bendelisis* and *B. barila*. He described them in *B. bendelisis* as: '. . . The chest is flattened and the scales in this region are poorly developed. There are characteristic muscular pads in front of the bases of the pectorals'. Dr Tyson Roberts reports (pers. comm.) that these pads are only evident in large, ripe males of this species, and that the epidermal surface of the pad is ridged transversely. A similar, but smaller, swollen area is found in some specimens of *Barilius zambesensis* and *B. ubangensis*. It seems likely that these pads may be used to steady the fish in fast flowing water. Perhaps significant in this respect is the comment on *Barilius bendelisis* made by Hora & Mukerji (1936): '. . . The pectoral fins are fan-like and horizontal and are never folded even when the fish moves from place to place. Some of the rays are especially strengthened and it seems likely that they are used either for digging in sand or for holding on to rocks in somewhat rapid waters.'

In view of the unknown distribution of this character amongst the cyprinids I am unable to ascribe to it any polarity, but I would suggest that it represents a derived character for a group of Indian *Barilius*. If the development of axial lobes is to be regarded as an apomorph condition (Howes, 1979), then *Opsariichthys*, *Zacco*, *Luciosoma*, *Barilius Group C* and some species of *Rasbora* would be linked by this character. Indeed, the development of the axial lobes and anal fin, together with the distinctive colour pattern, appear to be the only characters *Zacco* shares with the other bariliine and opsariichthine genera.

According to Nakamura (1969) it appears that the extended anal fin is used to mix the eggs and milt, which would suggest that this is a derived morphological character evolved in concert with a specialized reproductive behavioural pattern. There is no evidence at present to suggest that the marked sexual dimorphism apparent in the development of the anal fin is a plesiomorph character. Thus, if this character or character combination is viewed as synapomorphic, then *Zacco* must be united with other opsariichthine and bariliine genera, an action which would disregard other, perhaps more significant, osteological characters. Present indications are that *Zacco* is not closely related to the bariliine group (see p. 180) and so I consider this set of derived characters to be the result of convergent evolution in reproductive strategy.

Barbels

Opsariichthys

Barbels are present in one species, *O. barbatus*. This species was formerly assigned to the genus *Zacco*; reasons for placing it in *Opsariichthys* are discussed on p. 189. Only a single pair of minute posterior maxillary barbels is present.

Luciosoma

Two pairs of maxillary barbels are developed in all but one species. The rostral barbels are long and lie along the dorso-lateral border of the premaxilla and under the ventral edges of the 1st and

2nd infraorbitals. Each barbel stems from a thick pad of tissue which is connected by ligamentous strands to the edge of the 1st infraorbital. The tissue is embedded in the lateral groove of the maxilla and is intimately connected with the ligamentous bands which join the maxilla to the palatine. The insertion point of the *adductor mandibulae* A_1 muscle lies beneath the tissue pad but there is no direct connection and no muscle fibres run into the barbel. The barbel is innervated by a branch of the maxillary ramus of the trigemino-facialis nerve. The posterior maxillary barbel also stems from a thick fibrous pad, and is innervated by a branch of the nerve supplying the anterior barbel. The proximal head of the barbel is swollen and surrounded by bands of elastic-like tissue which extend along the outer border of the maxilla.

Barilius

In species of *Group A* barbels are present in one or two pairs, or are entirely absent. In *Group B* they are found in only one species, *B. guttatus*. In this species there is a minute barbel on the ventral border of the maxilla just below the anterior border of the 1st infraorbital and near the distal tip of the maxilla. Barbels are absent in species of *Group C*.

Engraulicypris

Barbels are absent.

Comments

It is perhaps significant that amongst the bariliines (see p. 180), reduction and absence of barbels is correlated with increased piscivorous specialization (cf. *Opsariichthys uncirostris* and *O. barbatus*; long-jawed *Barilius Group B & C* with short-jawed omnivorous *Barilius Group A*). Thus, the inference is that loss or reduction of barbels is a derived condition. Although barbels are widespread throughout the Cyprinoidei (again suggesting the plesiomorph condition) they are not a characteristic feature of the Cyprinidae. Contrary to Roberts' (1973) statement that 'Cyprinidae have one or two pairs of simple maxillary barbels', most of the species comprising the large assemblages of cultrine, cheline, alburnine, hemicultrine, aspinine and leuciscine groups do not have barbels. It could be argued that barbels are a derived feature. If this is so, then of those taxa presently under discussion, all the Indian and South-East Asian bariliines possessing barbels would have to be more closely related to barbine, or other carp groups, than to the African and Amur bariliines without barbels. From other anatomical evidence, this is clearly not the case. Where barbels are present in non-barbine or carp groups they appear, superficially, to be of a different morphological type. Gilbert & Bailey (1972) discussed the use of barbels in classifying some American cyprinids and concluded that this character was of little value as '... their diversity in position and structure points to repeated independent development and loss'. These authors discovered in American cyprinids at least six structural types, noting them as '... perhaps indicative of as many independent evolutionary lines'. The whole question of barbel morphology and homology in the cyprinids, and indeed in the ostariophysans, is obviously one to be investigated.

Roberts (1973) states that in cyprinids the movement of barbels is passive. This is not always so, for from personal observations on aquarium specimens of *Luciosoma* and *Leptobarbus* I can report that there is a definite movement of the posterior barbels which is independent of any jaw movement.

The brain

The possibility of using the gross morphology of the brain as a phylogenetic character was suggested by observations made by Dr R. Vari on various characoids and on *Opsariichthys* (pers. comm.).

The outstanding feature of the brain in *Opsariichthys* is the size and shape of the telencephalic lobes which are elongate, sausage-like structures separated from the mesencephalon by long posterior trabeculae. The usual situation in cyprinids, and it seems the majority of teleosts, is for the telencephalic lobes to be globular or ovate and closely apposed to the mesencephalon.

The olfactory bulb in *Opsariichthys*, and other cyprinids, is situated in the lateral ethmoid and thereby far removed from the telencephalon, the olfactory tracts being extended. Such extension of the olfactory tracts is also known in some characoids, in the siluroids, mormyroids and gadoids (Evans, 1940). It is known that in some cyprinids (e.g. *Carassius*) there is an ontogenetic change in the olfactory bulbs and tracts (Schnitzlein, 1964); in young specimens the olfactory bulbs are adjacent to the telencephalic lobes but with growth the olfactory tracts extend forward. As there is an actual lengthening of the tracts it appears that there is a disproportionate growth of parts of the cranium.

In small specimens of *Opsariichthys* the telencephalic hemispheres are large, occupy most of the orbitosphenoidal cavity and are well separated from the mesencephalon (Fig. 45A). The olfactory tracts are short and the bulbs located in the lateral ethmoids. In large specimens the telencephalic lobes, whilst still well separated from the mesencephalon, are more closely apposed and lie in the pterosphenoid; the olfactory tracts are long.

Thus, the difference between *Opsariichthys* and *Carassius* lies in the fact that although in *Opsariichthys* the olfactory lobes lie close to the telencephalon in early stages of development, it is the retreat of the telencephalon which gives rise to extension of the olfactory tracts whereas in *Carassius* (? and all other cyprinids) the telencephalon remains adjacent to the mesencephalon throughout growth. In a specimen of *Opsariichthys uncirostris amurensis* 82 mm SL the left telencephalic lobe is elongate and lies in advance of the right lobe, being connected to the mesencephalon by a long trabecula. In this and all other specimens examined the cerebellum is small.

Zacco and Barilius

The morphology of the brain in *Zacco* and *Barilius Groups A & B* is little different from that described in *Carassius* and *Cyprinus* by Evans (1940) and Schnitzlein (1964), i.e. the telencephalic lobes are rounded to ovate and separated from the mesencephalon by a deep recess (Fig. 45B). This condition appears to be invariable in the species examined. The olfactory tracts are long, slender and divergent anteriorly; the cerebellum is small.

In *Barilius Group C* there is a similarity to *Opsariichthys*. In *Barilius zambesensis* (Fig. 45D) and *B. ubangensis* the telencephalic lobes are elongate and separated from the mesencephalon by short posterior trabeculae. The same situation is found in *B. microcephalus* but in this species the olfactory tracts are thickened and the cerebellum large (Fig. 45C). In all species of this group the olfactory tracts lie close together and do not diverge anteriorly, the olfactory bulbs lie close together within the lateral ethmoids.

Engraulicypris is like *Barilius microcephalus* in the shape and size of the telencephalic lobes and the cerebellum (Fig. 45E). It should be noted here that the reference made by Evans (1940) to the particular brain morphotype of *Engraulicypris* refers only to the species *argenteus* assigned herein to *Rastrineobola* (see p. 195).

In *Leptocypris* the telencephalic lobes are also elongate but separated from the mesencephalon by a fissure; the olfactory bulbs are very large and the tracts short and thick. The cerebellum is larger than in any of the other genera examined.

The telencephalon of *Luciosoma* is small in comparison with the other genera, and the overall brain morphology resembles that of *Zacco*.

Comments

In functional terms the development of the telencephalon in *Opsariichthys* is unexplained. It is possible that the particular development of this part of the brain is in some way associated with integrating patterns of breeding behaviour of increased complexity (see Segaar, 1961; Nieuwenhuys, 1962). The usefulness of forebrain morphology as a phylogenetic character cannot be assessed, although from the apparently conservative morphological structure of the brain in other cyprinids, the condition in *Opsariichthys* possibly may be derived. The elongate telencephalic lobes, widely separated from the mesencephalon, is a feature shared with *Barilius Group C* species.

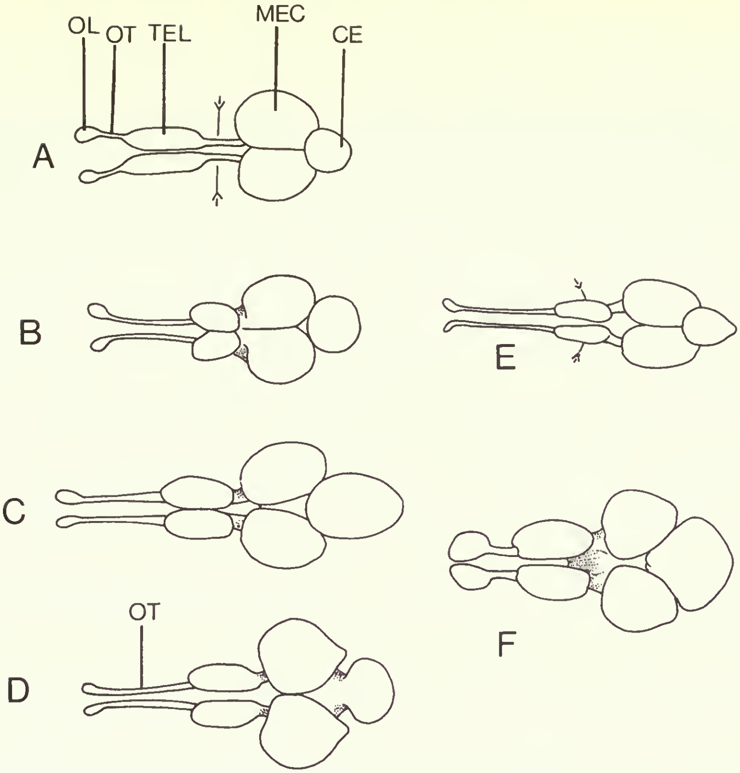


Fig. 45 Diagrams of the brain (dorsal views) in A. *Opsariichthys*. B. *Zacco platypus*. C. *Barilius microcephalus*. D. *Barilius zambesensis*. E. *Engraulicypris sardella*. F. *Luciosoma setigerum*. The arrowed lines indicate the suture between the orbito- and pterosphenoid.

Summary of character states

From the foregoing descriptions and analysis, the following characters are considered to be apomorph.

Narrow, deeply notched *supraethmoid*; shallow *mesethmoid*; small *preethmoid*; tubular olfactory foramen in *lateral ethmoid*; medially or distally expanded *kinethmoid*; ventrally thickened *vomer*; *pterosphenoid* contacting parasphenoid; *pterosphenoid* lateral fossa; enlarged *carotid foramen*; ventrally open *posterior myodome*; presence of a *jugular channel*; enlarged *sphenotic process*; reduced *dilatator fossa*; posteriorly extended *pterotic*; *posttemporal fossa* entering subtemporal fossa; narrow *frontal* with concave border; elongate *nasal* with more than 2 dorsal pores; elongate *parietal*; elongate *supraorbital*; narrow *infraorbitals*; anterior *maxillary* tips extended; anterior *maxillary* medial process ventrally directed; *dentary* notched anteriorly; *hyomandibular* condyles separated; *hyomandibular* lateral flange; *metapterygoid* process; small *symplectic*; *operculum* with elongate dorsal border; *cleithrum* with short upper part and expanded posterior lamina; *postcleithrum* reduced; *coracoids* in medial contact; 2*nd* and 3*rd centra* fused; *axial fin-lobes*; *reduction of barbels*; elongate *telencephalon.*

Relationships of the bariliine genera

Authors who have considered the systematic position and/or anatomy of *Opsariichthys* have assumed it to bear a close relationship to *Zacco* (see, for example, Regan, 1911; Takahasi, 1925; Ramaswami, 1955, Greenwood *et al.*, 1966; Bănărescu, 1968). This supposed relationship has been based upon the close similarity in external morphology of the two taxa which, in fact, resemble one another mainly in plesiomorph characters. None of the apomorphies identified here show *Opsariichthys* and *Zacco* to be sister taxa.

Characters identified as apomorphic in *Opsariichthys* also occur in *Barilius*, *Leptocypris*, *Engraulicypris*, *Luciosoma* and in some species of *Rasbora*. The synapomorphies which serve to identify these taxa as the **BARILIINE GROUP*** are:

1. Subtemporal fossa connected with the posttemporal fossa (in its most derived state the posttemporal 'fossa' is formed into a foramen, p. 146).
2. Posterior myodome open ventrally, with an external origin for part of the eye musculature (p. 153).
3. Anterior trigemino-facialis foramen situated entirely within the lateral face of the prootic (p. 153).
4. Frontal fossa (p. 155).
5. Lateral pterosphenoid fossa (p. 140).
6. Hyomandibula with widely separated condyles and lateral flange (p. 164).
7. Metapterygoid with dorsal posterior process (p. 165).
8. Pectoral and pelvic axial lobes or modified scales (p. 176).

Before the relationships of the bariliine genera can be understood, it is first necessary to discuss the classification of the genera *Barilius*, *Leptocypris*, *Engraulicypris* and *Rasbora* (in part).

Classification of *Barilius*

As previously recognized, *Barilius* has included both Indian and African species and although subgroups have been recognized (Günther, 1968; Day, 1877, 1889, see below) the 'monophyly' of the taxon has remained unquestioned. On the basis of characters here identified as apomorphic, *Barilius* is seen as polyphyletic. The following classification is not entirely satisfactory as not all the Indian species, and virtually none of those from Thailand and Burma, have been examined. Hopefully, however, the interim scheme presented will permit a more precise systematic evaluation of the various groups until such time as a complete taxonomic revision is attempted.

In the descriptive section of this paper three major groups (*A*, *B* and *C*) of *Barilius* are recognized. However, within *Group A* two subgroups can be identified, *viz.*:

1. *Barilius*. Termed in the descriptive section *Group A* and represented by the type species of the genus *Barilius barila* (Hamilton, 1822). It includes only those species inhabiting the Indian subcontinent, Thailand and possibly Burma. The genus is characterized by the apomorph features of a deep, rostrally curved ethmoid region, long nasals, long parietals, reduced lateral ethmoids and a deep frontal fossa.

Day (1877) recognized three groups of Indian *Barilius* characterized by the absence or presence and number of barbels (see p. 189). I recognize two groups, (i) exemplified by *Barilius barila* in which the jaws are long, the hyomandibular condyles well separated, scales with many radii, body shallow, barbels in two pairs, tubercles small and poorly developed; (ii) exemplified by *Barilius gatensis* in which the jaws are short, hyomandibular condyles barely separated, scales with few radii, body deep, a single pair of barbels, or barbels lacking, and tubercles large and well developed. As yet I have examined too few species to be certain if these groups represent part of a morphocline. The species contained in *Barilius* are listed on p. 189.

2. *Opsaridium*. Termed in the descriptive section *Group C* and represented by the type species of the genus *Opsaridium zambesense* (Peters, 1852). It includes only African species. The genus is characterized by the apomorph features of: an expanded kinethmoid; reduced premaxillary

---

* The use of the name bariliine for this assemblage follows Regan (1922) who first recognized the subfamily Bariliinae (see p. 185).

ascending process; anteriorly extended maxillary tips; deep frontal fossa; pterosphenoid cavity; extensive lateral temporal foramen; broad mesocoracoid and well-developed pectoral axial lobes.

The secondary sexual dimorphic characters of an extended anal fin in males, well-developed axial lobes and distinctively marked dorsal fin (see p. 191) serve to distinguish this genus from other related taxa. The species contained in *Opsaridium* are listed on p. 191.

3. *Raiamas*. Termed in the descriptive section as *Group B* and represented by the type species of the genus *Raiamas bola* (Hamilton, 1822). It includes both African, Indian, Burmese and Malaysian species. The genus is characterized by the apomorph features of: a greatly expanded kinethmoid; long shallow jaws; reduced premaxillary ascending process; extensive pterosphenoid-parasphenoid contact; small dilatator fossa; apophyseal platform formed partly from the prootics; extensive posttemporal foramen; long post-parietal platform; broad mesocoracoid; posteriorly extended cleithrum; elongate pectoral axial scale and extensive development of *adductor mandibulae* A2 muscle which laterally covers the *dilatator operculi* and *levator arcus palatini* muscles. Within this genus a transformation series represented by *R. loati–R. salmolucius–R. bola* is apparent in cranial elongation.

Previously (Howes, 1978) *Raiamas bola* was used as an example of bariliine anatomy when making comparisons with other cyprinids. It is now obvious that this species is not 'typical' of *Barilius* but represents a highly derived morphotype. Nevertheless, the conclusions reached in that study concerning the possible phylogenetic history of certain characters in *R. bola* remain valid within the hypothesis of relationships advanced here.

The inclusion of two Asian species in an otherwise entirely African genus requires some explanation. Four characters are present in *Raiamas bola* and *R. guttatus* which are lacking in their African congeners. These are: a closed posterior myodome; a much broader and S-shaped kinethmoid; extensive contact of the pterosphenoid and parasphenoid and, in *R. guttatus*, two pairs of small barbels. Possession of these characters in no way excludes *bola* and *guttatus* from inclusion in *Raiamas*. These two species are the most extreme members of their lineage in terms of cranial and jaw elongation, and are approached only by the African species *R. salmolucius* and *R. longirostris* (see p. 193). As mentioned above, a transformation series involving the lengthening of the pterosphenoid-parasphenoid suture, broadening of the kinethmoid and the secondary closure of the posterior myodome can be detected amongst the African species of *Raiamas* and the highly derived state of these characters in *R. bola* and *R. guttatus* is simply a continuation of this transformation sequence. It could, of course, be argued that the two Asian *Raiamas* species are simply the result of parallel evolution from an ancestral group of Indian bariliines. Such an hypothesis can be tested by identifying synapomorphies between *Raiamas* and *Barilius* and perhaps by showing a similar transformation sequence amongst the Indian bariliines. So far, I have found no such characters. The species contained in *Raiamas* are listed on p. 193.

The only species of *Barilius* occurring in the Middle East, *B. mesopotamicus* Berg, 1932, is, in fact, not a member of any of the genera listed above but should, on the basis of synapomorph characters, be included in the *Leucaspius* generic complex (see p. 190).

Classification of *Leptocypris*

Leptocypris has previously been recognized as monotypic; *Leptocypris brevirostris* Blgr, 1919 and *L. clupeoides* Pell., 1922 were synonymized with the type species *L. modestus* Blgr, 1900 by Poll & Gosse, 1963 and Gosse, 1966, respectively. The genus is characterized by its shallow lower jaw, the dentaries being joined at the symphysis by a ligament; inferior position of the mouth; pointed snout; deep, narrow and strongly curved ethmoid region; truncated lateral ethmoid; long, ventrally directed medial maxillary process; elongate parietal; elongate nasal opening; absence of, or reduced *intermandibularis* muscle; absence of, or reduced number of gill-rakers (3–6), and much elongated pectoral and pelvic axial scales.

Leptocypris possesses none of those apomorph characters which would suggest a close relationship with *Opsaridium* or *Raiamas* (i.e. extensive posttemporal fossa, broad kinethmoid and gutter-like metapterygoid process), but it does share some of those characters listed above with

Engraulicypris (see below). Additionally, it shares the features of an elongate supraorbital, and 1st infraorbital covering the anterior part of the 2nd infraorbital.

Two other species, formerly included in *Barilius*, *B. niloticus* (Joannis, 1835) and *B. weynsii* Blgr, 1899, share with *Leptocypris modestus* the apomorph characters listed above as characterizing the genus and are thus transferred here to *Leptocypris*. The characters distinguishing the three species are tabulated on p. 190.

Classification of *Engraulicypris*

As previously recognized, *Engraulicypris* has included several species of small-sized African cyprinids. However, the type species of the genus, *E. sardella* (Günther, 1868), possesses many apomorph characters, none of which are shared with any of the species presently included in *Engraulicypris*. For this reason the genus is restricted to the type species.

Engraulicypris is included in the bariliine group because it has characters 1, 2, 3, 4, 5 of those listed on p. 180 as typifying the group. The characteristic features of *Engraulicypris* are the extensively modified ethmoid region, the highly protrusile upper jaw and the long, numerous gill-rakers (total number 43–45).

The relationships of *Engraulicypris* with other members of the bariliine group are somewhat difficult to determine owing to the highly derived nature of many of its cranial features (autapomorphies). Other features, involving the pectoral girdle and vertebral column, are plesiomorphic and so offer no clues to relationship. On the basis of its possessing a well-developed pterosphenoid fossa and the trigemino-facialis foramen being situated in the lateral face of the prootic, *Engraulicypris* is included in a subgroup of the bariliine assemblage (see below, p. 184). *Engraulicypris* shares with *Leptocypris* elongate parietals; truncated lateral ethmoids; downwardly directed medial maxillary processes; an extensive 1st infraorbital bone overlapping the anterior part of the 2nd infraorbital; elongate supraorbital; ligamentous connection of the dentaries and an elongate pelvic axial scale. In both *Engraulicypris* and *Leptocypris* the subtemporal fossa is narrowly conical with only a small foramen leading into the posttemporal fossa. The small opening is suggestive of a 'precursory' condition leading to the intramural channel and extensive foramen found in other bariliine genera.

Engraulicypris and *Leptocypris* are here regarded as sister genera forming a branch of the bariliine assemblage (see below). Which of the two can be considered the more divergently specialized is debatable. Certainly *Leptocypris* is trophically more generalized. Matthes (1963) made the point that *Leptocypris* was probably derived from *Barilius*-like ancestors and although more generalized than *Barilius* did not necessarily represent a primitive form. Matthes' concept of *Barilius* differs from that presented here and the '*Barilius*' species he was comparing with *Leptocypris* are now considered as members of the relatively derived groups *Opsaridium* and *Raiamas*. I would agree with Matthes that *Leptocypris* is not 'primitive' (plesiomorph) and further point out that there is a morphocline in this genus toward a carnivorous type represented by *L. weynsii*. The suggestion made by Goren *et al.* (1973) that *Engraulicypris* is derived from *Barilius* cannot be accepted as these authors too were considering polyphyletic assemblages.

Classification of *Rasbora* (in part)

Throughout the descriptive section mention has been made of supposedly derived characters shared between *Luciosoma* and some species of *Rasbora*. These characters are: supraethmoid with a broad bowl-shaped depression; an expanded kinethmoid; a deeply concave vomer; a tubular olfactory foramen in the lateral ethmoid; an inflated orbital portion of the lateral ethmoid; a well-developed symphysial knob on the dentary followed by a deep notch; an elongate lateral occipital fenestra; a long operculum; elongate ceratobranchials, and a pectoral axial lobe attached to the postcleithrum. As well as these features, the *Rasbora* species possess characters 1, 4 and 5 of those identifying all bariliine genera. Within this '*Rasbora*' complex, two closely related groups can be identified. One group is referred to a new genus, *Parluciosoma* (see below), and the other to *Megarasbora* Gunther, 1868.

PARLUCIOSOMA gen. nov.

Rasbora (in part) Hamilton, 1822

TYPE SPECIES: *Leuciscus argyrotaenia* Bleeker, 1850.

In his revision of *Rasbora*, Brittan (1954) recognized an assemblage of species which he named 'The *argyrotaenia* complex'. He distinguished this from other species complexes within the genus by their medium to large size and by '. . . conservative structure and color-pattern'. Brittan (1954) did not explain the precise nature of their 'conservatism' and whilst it is true that nearly all members of the group display a distinctive colour pattern comprising a black lateral stripe and dark edges to the caudal fin (in preserved specimens), this character is of little value in formulating relationships. More significant in this regard are the osteological characters which this group of '*Rasbora*' shares with *Luciosoma*: ethmoid region broad, the supraethmoid with a bowl-shaped depression, the kinethmoid compressed and expanded distally; the dentary with a well-developed symphysial process; the maxilla with an extended anterior tip narrowly separated from its fellow medially; the premaxilla with a short anterior ascending process; the frontal with a ventral fossa (and in one species, *P. dusonensis*, a lateral groove as in *Luciosoma*; see p. 155); a bony tube surrounding the olfactory foramen in the lateral ethmoid; elongate lateral occipital fenestra; the operculum broad and somewhat attenuated, and a well-developed pectoral axial lobe attached to the postcleithrum. Barbels are lacking.

Parluciosoma differs from *Luciosoma* in having a shallower supraethmoid depression, a narrow contact between the parasphenoid and pterosphenoid, shorter lateral processes of the 2nd vertebra and a long, medially directed postcleithrum. The jaws also tend to be shorter and deeper with a stronger symphysial notch on the dentary. The species contained in *Parluciosoma* are listed on p. 194, and the relationships of *Rasbora* (*sensu stricto*) are discussed on p. 185.

MEGARASBORA Günther, 1868

TYPE SPECIES: *Cyprinus elanga* Hamilton-Buchanan, 1822.

Megarasbora was used by Günther (1868) in a subgeneric sense to include *Rasbora elanga*. Brittan (1954) noted that *R. elanga* 'is discontinuous with the remainder of the species in the genus'. He drew attention to the short pair of rostral barbels and the 'peculiar' striae and ridges of the scales as well as to the high number of lateral line scales (40–44) compared with other *Rasbora* species. However, when compared with *Luciosoma* these characters are in concordance.

Megarasbora is characterized by a broad ethmoid region, the supraethmoid with a semicircular depression; the kinethmoid lamellar; the premaxilla with a long, slender medial anterior process; the sphenotic with a broad lateral process which contains a fossa in its anterior face; the dilatator fossa confined to the sphenotic; the dentary with a deeply concave notch posterior to the symphysial process; the lateral process of the 2nd vertebra containing a ventral fossa; the postcleithrum short and supporting a poorly developed axial lobe; pharyngeal teeth with strongly recurved tips (dental formula: 4.3.2); total number of gill-rakers on 1st gill arch, 8–9.

Megarasbora differs from *Luciosoma* and *Parluciosoma* in the nature of the characters enumerated above and in possessing a pair of short maxillary barbels, more obliquely aligned jaws and almost complete lack of body and fin markings. The genus is monotypic; see p. 195 for distribution.

Interrelationships and classification of the bariliine genera

The synapomorph characters identified in the foregoing anatomical descriptions (listed on p. 180) serve to relate *Barilius*, *Leptocypris*, *Engraulicypris*, *Opsariichthys*, *Opsaridium*, *Raiamas*, *Megarasbora*, *Parluciosoma* and *Luciosoma* as a monophyletic unit termed the *bariliine group* (see p. 180). The taxa comprising this group can be classified into two assemblages related as sister groups:

1. The bariliine assemblage (*Barilius*, *Leptocypris*, *Engraulicypris*, *Opsariichthys*, *Opsaridium* and *Raiamas*) defined by those characters listed on p. 180.

2. The luciosomine assemblage (*Luciosoma*, *Parluciosoma* and *Megarasbora*) which lacks a ventrally open posterior myodome. In addition to the derived characters shared with the bariliines (nos 1, 3, 4, 5 and 8 of those listed on p. 180), the luciosomines possess the autapomorphic features of: supraethmoid with bowl-shaped depression; compressed and medially expanded kinethmoid; lateral ethmoid inflated posteriorly and containing a tubular olfactory foramen; elongate lateral occipital fenestra and a pectoral axial fin lobe attached to the postcleithrum.

Within these two assemblages various sub-groups or lineages can be recognized as follows:

Bariliine assemblage

Barilius represents the lineage which forms the sister group to the other members of the assemblage. This taxon possesses all the characters listed on p. 180 as defining the group apart from 3 and 7. *Barilius* is distinguished from other included taxa by the apomorph characters of: a deep, strongly curved and narrow ethmoid region; elongate nasals; elongate parietals and truncated lateral ethmoids.

Leptocypris, *Engraulicypris*, *Opsariichthys*, *Opsaridium* and *Raiamas* represent the apomorph sister group to *Barilius*. These genera are linked by the synapomorphies: pterosphenoid fossa and anterior trigemino-facialis foramen situated in the lateral face of the prootic.

Leptocypris and *Engraulicypris* together form the sister group to the other three genera and possess the synapomorphies: ventrally directed medial maxillary process; elongate supraorbital; 1st infraorbital partially overlapping the 2nd infraorbital and elongate pelvic scale.

Opsaridium, *Opsariichthys* and *Raiamas* possess the synapomorphies: anteriorly extended maxilla; bulbous vomer; presence of quadrate flange and lateral temporal foramen.

Opsaridium and *Raiamas* form the apomorph sister group to *Opsariichthys* linked by the synapomorphies: dorsally expanded kinethmoid; broad mesocoracoid and extensive posttemporal foramen.

Luciosomine assemblage

Parluciosoma and *Luciosoma* form the apomorph sister group to *Megarasbora*. Apomorphies characterizing and linking these genera have already been discussed (p. 183).

The relationships of the genera forming the bariliine group are shown as a cladogram in Fig. 46.

When dealing previously with monophyletic groups of cyprinids (Howes, 1978, 1979) I refrained from assigning them to formal taxonomic categories and presented them as 'informal groups'. This same policy is followed here and for the same reasons, i.e. lack of congruency at higher level classification. The nature of the cladistic classification tends to inflate hierarchical levels. Thus, when the interrelationships of the bariliine group with those of other monophyletic assemblages are more completely understood it is likely that some of these groups, including the bariliines, will have to be assigned subfamily status.

Interrelationships of the bariliine group

The search for the sister group of the bariliines has so far proved inconclusive. The reason is that the majority of cyprinid subfamilies, and even genera, currently recognised are non-monophyletic in the cladistic sense and it has not been possible to postulate relationships on the basis of synapomorphic characters. In previous studies I identified some monophyletic lineages (Howes, 1978, 1979) and in dealing with one of these groups, the chelines, I stated that there was no evidence to suggest close relationship with the bariliines (Howes, 1979). Since then, however, this hypothesis has been weakened by the identification of presumed synapomorphies associated with the jaws and otic region of the cranium (work in preparation). Regan (1911) suggested a relationship between *Barilius*, *Danio* and *Opsariichthys* considering that these genera were related to *Aspius* and *Leuciscus*, and stated '. . . *Hypophthalmichthys* is nearly related to the *Barilius* group'. Later, Regan (1922) considered the geographical distribution of the Cyprinidae and recognized the Bariliinae as the most primitive members of the family. In this work Regan noted that there were a few Palaearctic genera in the Bariliinae, but he did not name them. Furthermore, he was quite explicit with regard to their relationships '. . . the Leuciscine Cyprinidae is derived from the more primitive and more southern Bariliinae'.

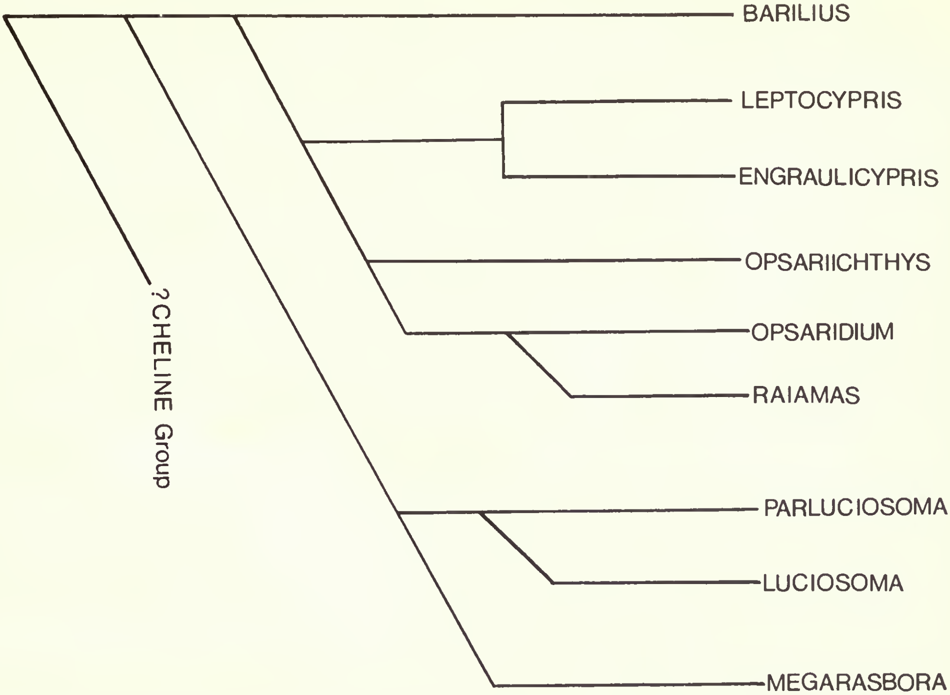


Fig. 46 Cladogram illustrating the relationships of the bariliine genera.

The evidence presented here falsifies Regan's claim for a close association between the leuciscines and bariliines. Neither have any synapomorphies been identified which relate *Hypophthalmichthys* with any bariliine taxon. As remarked previously (Howes, 1978) the Leuciscinae are a polyphyletic assemblage including at least three major groups. Current studies indicate that these three groups can be related at various levels to the aspinines, cultrines and hemicultrines (including the Xenocyprininae) *sensu* Howes (1978, 1979). In turn, this higher-level group appears as the likely sister group to that comprising the bariliines, chelines, rasborines and danioines. The interrelationships of the various monophyletic subgroups have yet to be deduced.

Matthes (1963) considered that the '. . . "*Barbus* and *Barilius*" types share many characteristics which are indicative of close phylogenetical affinities'. I have found no synapomorph characters indicating close relationship of the bariliines with any barbine or labeine group.

Gosline (1978) considered *Opsariichthys* and *Zacco* to be 'specialized' genera allied with the 'cultrin series of Leuciscinae, but with indications of affinity with the *Tribolodon*–American section of the subfamily'. Gosline gives no clue as to what these 'indications of affinity' might be. The tacit implication of this statement is that the American and Asian 'Leuciscinae' are a monophyletic assemblage. My opinion, based on current investigations of the anatomy of *Tribolodon*, is that this genus is indeed related to a group of the American cyprinids (including *Ptychocheilus*), but that the sister group to this assemblage is, in all probability, the aspinine group *sensu* Howes (1978). There is certainly no indication in terms of shared derived characters of any close relationship between any member of the bariliine group and the *Tribolodon*–American assemblage.

Finally, mention must be made of *Zacco* which in the absence of synapomorphous osteological characters is excluded from the bariliine group. It must be admitted that as yet I have been unable to relate *Zacco* with another monophyletic group. Indications are, however, that derived characters associated with the ethmoid and otic regions of the cranium are shared with members of the alburnine assemblage of 'Leuciscinae'.

Biogeography of the bariliines

The bariliine group is represented in Africa, India, Burma, the Amur basin, Korea, Japan (Honshu Island only) and the south-east Asian archipelago. Both plesiomorph and derived taxa occur sympatrically in Africa and India. The present distribution and almost complete allopatry of the derived members of the bariliine (*Opsariichthys* and Indian *Raiamas*) and luciosomine (*Luciosoma*) assemblages indicates vicariance events occurring after the break-up of Gondwanaland.

The geographical distribution of the bariliines in Africa is as follows:

Opsaridium occurs in the Zambesi drainage and Lake Malawi, extends south to the Limpopo river and north through Zaire to the Ja (Dja) river, as far west as the Cubango river, and east to the Rufiji. *Opsaridium* is the only bariliine genus found in the Zambesi basin and the east-African drainage systems (see Banister & Clarke, in press, for detailed distribution).

Leptocypris and *Raiamas* both have similar distribution patterns, ranging through the Nilo-Sudanian and Zairean provinces. *Raiamas* extends far to the west in Sierra Leone while its most southerly distribution is to Lake Tanganyika.

Engraulicypris is confined to Lake Malawi.

The partially sympatric distribution of the bariliine genera in Africa suggest a series of vicariance events, with the most derived genus, *Raiamas*, being the most widely distributed. *Engraulicypris* is the only bariliine adapted to a planktonophagous niche, this niche in other Rift lakes being occupied by derivates of a Euro-Asian assemblage of cyprinids (see p. 196).

The pattern of bariliine distribution in India shows that the relatively plesiomorph species *Barilius bendelisis* and *B. vagra* are widely distributed and indeed are the only *Barilius* species found in the Indus plain (Mirza, 1974) and Sri Lanka (Silas, 1953). *Raiamas* extends eastward, beyond the range of *Barilius* into Shan and the Malay Peninsula.

Plesiomorph luciosomines (*Parluciosoma* and *Megarasobra*) are also present in India with the more derived species of *Luciosoma* and *Parluciosoma* extending through the Malay Peninsula and along the Sunda Island chain.

Opsariichthys occurs through southern China, the Amur basin, Korea and Honshu Island of Japan. What may prove to be the more plesiomorph species of *Opsariichthys* inhabit Taiwan and Hainan (see p. 189).

The affinity of the Indian with the Malaysian ichthyofauna has been emphasized by Hora (1944) and Menon (1953, 1955). In Menon's view, Indian ostariophysi had their 'origins' in southern China and dispersed along the Himalayas and the Burma–Malayan arc. More recently Briggs (1979) has made a similar assertion that the cyprinoids had their origins in the Oriental Region, more particularly in South-East Asia. These hypotheses suffer from not having as their base-line a well-founded theory of phylogenetic relationship. Furthermore, it seems that these ideas depend upon the ancestral lineages of the present-day ostariophysan groups having been confined to 'evolutionary centres' from which they dispersed (Briggs, 1979). The difficulties inherent in constructing 'dispersal' hypotheses on the basis of palaeogeography are realized when considering the varying views concerning the Gondwanic position of the South-East Asian block and its likely connections with India. Burton's (1970) and Ridd's (1971) proposals are for juxtaposition of the Malay Peninsula with India, whereas Stauffer (1973) considers the Malayan blocks as once having African connections.

The system of interrelationships hypothesized here for the bariliines suggests a Gondwanic (i.e. pre-drift India+Africa) distribution (Fig. 47). Banister & Clarke (1977), in accounting for a Gondwanic distribution of another ostariophysan group, the Clariidae, were puzzled by the narrower geographical gap separating the Indian and African *Barilius* compared with that separating the *Clarias* of the two continents. These authors had been misled by the misidentification of a middle-Eastern cyprinid as a *Barilius* (see p. 190). Now it is seen that the distribution of the bariliines approximates closely to that of the Clariidae and to that of two other cyprinid groups, the barbines and labeines. However, before too many assertions can be made concerning the distributional history of the cyprinids, the monophyletic integrity of these two groups must be tested, as indeed must that of the entire Cyprinoidei.

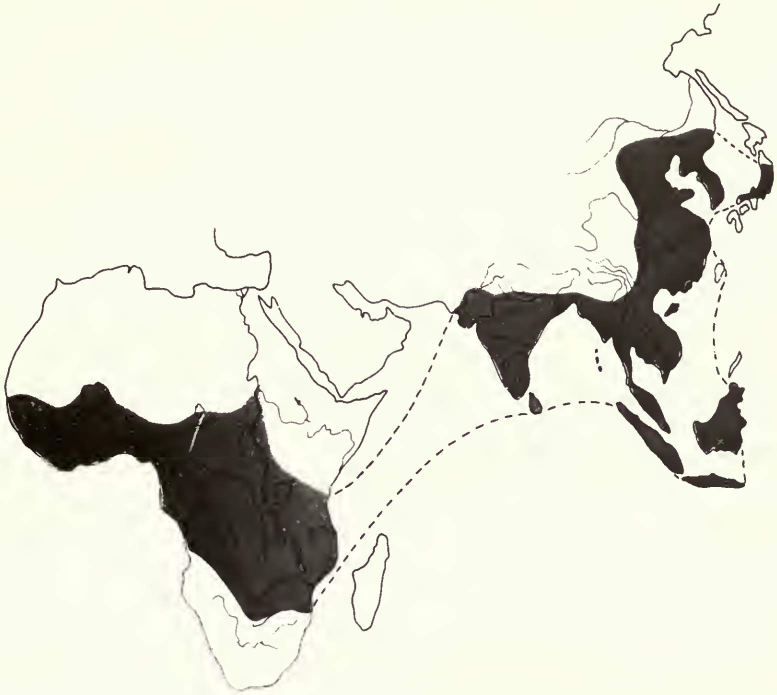


Fig. 47 Map showing distribution of bariliine genera (dark grey) and dispersal track (broken line). Blanket coverage is given to Sumatra, Java and Borneo although the actual distribution of bariliines on these islands is still to be ascertained.

Conclusions

1. *Opsariichthys* is not a 'primitive' cyprinid – the opinion of previous authors – but a relatively derived member of its group.
2. *Opsariichthys* is a member of a monophyletic unit termed the *bariliine group* comprising two sister assemblages whose constituent genera are: *Luciosoma*, *Parluciosoma* and *Megarasbora*; and *Barilius*, *Leptocypris*, *Engraulicypris*, *Opsariichthys*, *Opsaridium* and *Raiamas*.
3. *Barilius* as previously conceived was a composite genus, it is here restricted to include only those species inhabiting the Indian subcontinent and parts of South-East Asia. Most of the species formerly included in *Barilius* are assigned to *Opsaridium*, *Raiamas* and *Leptocypris*, others are found to possess apomorph characters which relate them to other cyprinid genera.
4. *Engraulicypris* as formerly recognized is a composite genus. It is here restricted to include only the type species, *E. sardella*. This is a derived member of a lineage within the bariliine assemblage whose sister taxon is identified as *Leptocypris*. The other species formerly included in *Engraulicypris* are assigned to various non-bariliine genera (see Appendix 2).
5. *Rasbora* is a composite genus and includes a monophyletic assemblage typified by *R. argyrotaenia* here described as a new genus, *Parluciosoma*. This taxon is the sister group to *Luciosoma* and together they form the sister lineage to *Megarasbora*.

6. Transition series of characters correlated with cranial elongation are identified in both the bariliine and luciosomine clades.
7. The interrelationships of the bariliine group are unresolved although preliminary (unpublished) evidence suggests that they are the sister group to the chelines (*sensu* Howes, 1979).

Acknowledgements

I am most grateful to all my colleagues in the Fish Section of the British Museum (Natural History) for their assistance during this work. In particular Drs Humphry Greenwood and Keith Banister have aided by means of their stimulating and fruitful discussions and their criticims of the manuscript. In this regard I must thank Dr Gordon Reid who also permitted me to use some of his unpublished findings concerning the use of cyprinid tubercles.

My sincere thanks are due to Dr Tyson Roberts for providing me with information on Indian and African bariliines and to Drs Max Poll and C. Lavett-Smith for allowing me to borrow the type specimens then under their care of, respectively, *Engraulicypris katangae* and *E. congicus*.

Finally, special thanks to Gina Sandford for typing the manuscript and to Jeff Jacobs for obtaining for me a live (which subsequently became a dead) specimen of *Luciosoma trinema*.

Appendix 1

Annotated list of bariliine genera and species

The following notes concerning the taxonomy of the bariliine taxa are in no way intended as a formal revision but serve to indicate the assignment of species to the genera as now defined. In the course of this study it has been necessary to examine type specimens of many of the species included in the group and some discrepancies in earlier descriptions have been corrected in the light of these examinations.

OPSARIICHTHYS Bleeker, 1863

TYPE SPECIES: *Leuciscus uncirostris* Temminck & Schlegel, 1844.

DISTRIBUTION: Northern, central and southern China, Southern tributaries of the Amur, Korea, Japan (Honshu), Hainan and Taiwan.

Bănărescu (1968) appears to be the only author to have revised the genus. This revision was in effect a note on the so-called subspecies of *Opsariichthys*. Bănărescu (1968) made no attempt to define the genus and failed to recognize that two species placed in the genus *Zacco* in fact belong with *Opsariichthys*. These are the species *pachycephalus* Günther, 1868 and *barbatus* Regan, 1908 (see below). I have the following remarks to make concerning the three species now assigned to the genus:

Opsariichthys uncirostris (Temminck & Schlegal, 1844)

Bănărescu (1968) follows Nichols (1943), Berg (1949) and Wu (1964) in recognizing other nominal species of the genus as being subspecies of *O. uncirostris*. The separation of the subspecies appears to have been made only on the basis of the number of lateral line scales, a character in which there is complete overlap throughout the range of the species. Other characters such as the varying morphology of the jaw, cranial osteology and buccal epidermis have been completely disregarded by previous authors.

Opsariichthys pachycephalus Günther, 1868

This species has been placed in *Zacco* by various authors but is, in my opinion, a member of *Opsariichthys*. It shares with other species of the genus the notched lower jaw; a metapterygoid process; separated hyomandibular condyles; a hyomandibular flange; pterosphenoid-parasphenoid connection; subtemporal fossa connected with posttemporal fossa; deep infraorbitals; maxilla narrowly separated from the premaxilla. It does not share with *Zacco* the deep, narrow ethmoid block, enlarged carotid foramen nor the produced anterior cleithral lamina.

Opsariichthys pachycephalus differs from other species in its low number of vertebrae (40 cf. 44 in *uncirostris* and 42 in *barbatus*) there being fewer caudal vertebrae (17–18) than in all other bariliine taxa except *Luciosoma* and *Parluciosoma* (16–17).

Bănărescu (1968) notes that specimens recorded from Taiwan as *Zacco temmincki* or *Zacco platypus* are most probably misidentified and should be referred to *Opsariichthys pachycephalus*.

Opsariichthys barbatus Regan, 1908

This species is recorded only from Lake Candidus on Taiwan and was placed by Jordan & Richardson (1909) in a separate genus *Candida* on the basis of possessing a pair of posterior maxillary barbels. Bănărescu (1968) included the species in *Zacco*, considering the presence of barbels insufficient evidence to warrant generic status. However, Bănărescu had overlooked the form of the lower jaw which is quite different from that of *Zacco*. I disagree with Bănărescu's (1968) assignment of the species *barbatus* to *Zacco* and believe that it should be placed in *Opsariichthys*. Having only the type specimens available I have been unable to check that all the osteological characters necessary for inclusion in this genus are present. However, from radiographs it is clear that the cranium and pectoral girdle have an overall opsariichthine-morphology (the ethmoid block is broad and shallow and a metapterygoid process is present).

The lower jaw of *O. barbatus* is shorter than that in any other *Opsariichthys* species and is completely overlapped by the upper jaw when the mouth is closed (Fig. 48). The jaw is also inclined at a more oblique angle so that its articulation with the quadrate comes to lie on a line passing through the centre of the orbit whereas in other *Opsariichthys* it is below the posterior third of the orbit. The lateral line scales number 54–56, is comparable only to that in *O. pachycephalus* (53) and *O. uncirostris uncirostris* (50–59).

Jaw morphology and low vertebral numbers suggest that *Opsariichthys pachycephalus* and *O. barbatus* are relatively plesiomorph species as compared with *O. uncirostris*. However, the interrelationships of the three species can only be resolved when osteological material of *O. pachycephalus* and *O. barbatus* is available and synapomorphies are identified. Meanwhile, I would hypothesize that the two Taiwan species form the plesiomorph sister group to the *Opsariichthys uncirostris* species complex of China, Japan and the Amur basin.

BARILIUS Hamilton, 1822

TYPE SPECIES: *Cyprinus barila* Hamilton, 1822.

The genus as now restricted includes only those species occurring in India, Sri Lanka, Burma and Thailand.

Hamilton (1822) first used *Barilius* as a 'Division' of *Cyprinus* under which he included *B. barila*, noting that it lacked barbels. Heckel (1842) apparently overlooked or disregarded Hamilton's use of *Barilius* and proposed *Pachystomus* in which he included species with 4 barbels and those without barbels.

Bleeker (1849) introduced *Bendelisis* as a subgenus of *Barilius* to include species with 2 barbels. Later, in the *Atlas* (1863) he designated the species *bendelisis* as the type of the subgenus, stating 'cirri 2'. However, Bleeker was in error as *B. bendelisis* (Hamilton) has 4 barbels.

Day (1877) used *Pachystomus*, *Bendelisis* and *Barilius* as divisions of *Barilius*. Species with 4 barbels he included in *Pachystomus*, species with 2 barbels in *Bendelisis* and those without barbels in *Barilius*. Day (1877) included only a single species in *Bendelisis*, namely *barila*. But, Day too was in error as *B. barila* also has 4 barbels. (Day's mistake was pointed out by Hora, 1921.) At the same time, Day (1877) noticed Bleeker's previous oversight with respect to the number of barbels in *B. bendelisis* (see above) and placed the species in *Pachystomus*. Finally, Jordan (1919) designated *barila* as the type species of *Barilius* by logotypy.

Thus, it would appear that *Pachystomus* and *Bendelisis* are synonyms of *Barilius*.

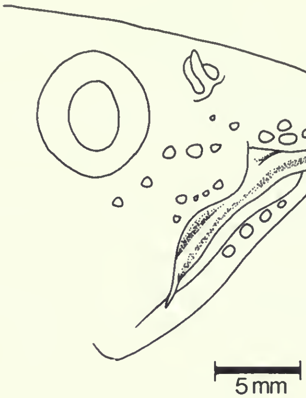


Fig. 48 *Opsariichthys barbatus*, lateral view of the head to show form of the lower jaw.

As noted above, p. 180, two groups of *Barilius* can be recognized, but it is possible that these 'groups' form part of a morphocline. Included species: group (i): *B. barila* (Hamilton, 1822), *B. bendelisis* (Buchanan, 1807), *B. radiolatus* Günther, 1864, *B. vagra* (Hamilton, 1822), *B. shacra* (Hamilton, 1822); group (ii): *B. bakeri* (Günther, 1868), *B. barna* (Hamilton, 1922), *B. canarensis* (Jerdon, 1849), *B. evezardi* Day, 1872, *B. gatensis* (Val., 1844), *B. modestus* (McCl., 1842), *B. ornatus* Sauvage, 1883, *B. tilheo* (Hamilton, 1822).

The following species are ones which I have not examined and am unable to allocate with certainty to *Barilius*: *B. bernatziki* Koumans, 1937, *B. dogasinghi* Hora, 1921, *B. huahinensis* Fowler, 1934, *B. infrafasciatus* Fowler, 1934, *B. karatensis* Smith, 1931, *B. pulchellus* Smith, 1931, *B. ponticulus* (Smith, 1945), *B. nanensis* Smith, 1945.

Two other species formerly placed in *Barilius* are found not to belong to this genus; they are:

Barilius auropurpureus Annandale, 1918 from Inle Lake, Burma, possesses characters which relate it to the cheline group.

Barilius mesopotamicus Berg, 1933 possesses apomorph characters shared with some species presently assigned to *Leucaspius*.

LEPTOCYPRIS Boulenger, 1900

TYPE SPECIES: *L. modestus* Boulenger, 1900.

DISTRIBUTION: Africa; Nile, Niger and Zaire.

Two other species are included in the genus, *L. niloticus* (Joannis, 1835) and *L. weynsii* (Blgr., 1899). The characters distinguishing the three species are as follows:

	L. niloticus	*L. modestus*	*L. weynsii*
Gill-rakers on 1st ceratobranchial	3	0	2–3
Lateral line scales	36–40	40–42	44–45
Anal fin rays, branched	11–12	8–9	14–15
Maxillary valve	non-papillate	papillate	non-papillate
Pelvic scale, % of pelvic fin length	25	75	75
Extent of maxilla	to centre of eye	anterior	centre

Barilius guineensis Daget, 1962 appears from the description and figure also to belong to *Leptocypris*. Characteristic are the inferior position of the mouth and rather prominent snout. Daget (1962) notes the close similarity between *B. guineensis* and *B. weynsii*.

ENGRAULICYPRIS Boulenger, 1911

TYPE AND ONLY SPECIES: *Barilius sardella* Günther, 1868.

DISTRIBUTION: Lake Malawi and upper Shire river.

OPSARIDIUM Peters, 1852

Pelotrophus Günther, 1864.
Barilius (non Hamilton), Boulenger, 1899 (part).

TYPE SPECIES: *Leuciscus zambesensis* Peters, 1852.

DISTRIBUTION: Africa; Zambesi, Zaire, Quanza and Lower Guinea provinces (Roberts, 1975).

Opsaridium is the plesiomorph sister taxon to *Raiamas* and is characterized by an extended anal fin in the males, larger and granular tubercles, large and well-patterned dorsal fin (13–15 branched rays) and fleshy or lobate pectoral axial scales. Osteological characters are listed on p. 180.

Included species: *O. zambesense* (Peters, 1852), *O. christyi* (Blgr, 1920), *O. loveridgi* (Norman, 1922), *O. microcephalus* (Gnthr, 1864), *O. microlepis* (Gnthr, 1864), *O. ubangense* (Pellegrin, 1901).

Opsaridium zambesense (Peters) and *O. ubangense* (Pell.)

On the basis of their external morphology and osteology these two species appear to be closely related. Indeed, in Boulenger's (1911) key there is a complete overlap of diagnostic characters. Jubb (1967) placed *Barilius neavii* Blgr, 1907 and *B. peringueyi* Gilchrist, 1913 into the synonymy of *B. zambesensis*, stating that these 'species' represented various growth stages.

I have examined all the specimens in the BM(NH) collections identified as *B. zambesensis* and *B. ubangensis* and have the following comments to make: In *Opsaridium zambesense* (as represented by the types and the types of *Barilius neavii*) the maxilla extends as far as the suture of the 2nd and 3rd infraorbitals, the operculum is long and rather attenuated, the dorsal fin is patterned by dark bands of pigment extending between the rays, except the 6th to 8th rays where the pigment is confined to the distal margin of the fin membrane. (This pattern is admirably illustrated in Poll, 1967, fig. 89.) The pectoral axial scale is small with a fleshy lower margin, the dark bars along the flanks are almost always split anteriorly and number 6–12, lateral line scales number 41–43. The pectoral axial lobe is small; the dark bars along the flanks are almost always split anteriorly and number 6–12, lateral line scales number 41–43.

Specimens from the Cubango river, Angola (BMNH 1965.3.15 : 34–39) previously determined as *B. zambesensis* differ from the above description on having somewhat longer jaws, longer operculum and a clear submarginal band on the dorsal fin.

In *Opsaridium ubangense* (specimens from Ubanghi, Luala and Luluaburg), the maxilla extends to just beyond the anterior border of the eye, the operculum is short, the dorsal fin is similarly patterned to that in *O. zambesense* except that the dorsal anterior margin is without pigment and the tips of the membrane between the last two rays is very dark. The pectoral axial scale is fleshy and short, the dark bars along the flanks are split and number 12–13, lateral line scales number 39–42.

Specimens identified as *O. ubangense* from the Kribi and Ja (Dja) rivers (Cameroon) differ from 'typical' *O. ubangense* in that the 3rd and 4th infraorbitals are broad, almost covering the cheek, the pectoral axial lobes are longer and the dorsal fin lacks the intensely dark posterior distal markings.

Specimens from the Upper Mwanza and Upper Shire rivers are also identified as belonging to the *O. ubangense* group.

At present the limits of the various taxa included within the *zambesense–ubangense* complex cannot be defined and the problem may only be resolved when further, larger samples from a wider geographical area become available.

Opsaridium loveridgi (Norman, 1922)

Described from a single specimen from the Rufiji river, the fish has a well-developed pectoral axial lobe and colour pattern characteristic of the genus *Opsaridium*. Norman (1922) noted that the species was '. . . Near *B. ubangensis* and *B. peringueyi*'. Certainly *O. loveridgi* belongs to the *O. ubangense–zambesense* group but appears to be a distinct species.

Opsaridium microcephalus (Gnthr, 1864) and *O. microlepis* (Gnthr, 1864)

These two species both occur in Lake Malawi. Günther (1864) referred them to the genus *Pelotrophus* on account of their extended anal fins.

Opsaridium microcephalus differs from other *Opsaridium* species in possessing a ventral frontal foramen and an extensive lateral temporal foramen (p. 147, Fig. 17). It shares with *O. microlepis* a high vertebral number (47–48) and a high number of dorsal fin rays (15–17).

The relationships of the Lake Malawi species have not yet been explored in great depth but indications are that the closest riverine relative is *O. ubangense*.

Three species formerly included in *Barilius* are recorded from Lake Tanganyika; *moori*, *salmolucius* and *tanganicae* (Poll, 1953; Worthington & Ricardo, 1936). The first two species are now included in *Raiamas* (see below) but *tanganicae* has an *Opsaridium*-like morphology. *Barilius tanganicae* Blgr, 1900 is known only from the holotype, and despite subsequent collecting no specimens have been recorded again. Poll (1953) makes no mention of the species; Worthington & Ricardo (1936) note only the type. The holotype conforms in almost every respect to the description of *Barilius microlepis* given by Boulenger (1911). Although Boulenger (1911) states for *tanganicae* '. . . 16 or 17 blackish vertical bars on each side of the body' and for *microlepis* '. . . no markings', there are in fact similar markings present in *microlepis* (see Poll, 1953).

The holotype of *B. tanganicae* was collected by J. E. S. Moore and bears the BMNH register number 1906.9.6 : 26. The locality given in the accessions register is 'N end of L. Tanganyika'. Regrettably there is no collection number or label which can help to identify the locality. In view of the fact that Moore's locality labels have proved to be unreliable in the past (see Trewavas, 1946 : 244) I suspect that *tanganicae* is a specimen of *microlepis* and that it was collected from Lake Nyasa (L. Malawi). Thus, until there is evidence to the contrary I place *Barilius tanganicae* into the synonymy of *Opsaridium microlepis*. This means that the only bariliine species known from Lake Tanganyika are of the genus *Raiamas*.

Species which I have not examined but which appear from the literature to belong to *Opsaridium* are: *Barilius maculicauda* Pellegrin, 1926. Described from 3 specimens collected at Tshikapa, Congo. The description and Pellegrin's observation that the species resembles *O. zambesense* indicate its inclusion in *Opsaridium*.

Barilius leleupi Matthes, 1965. The prolongation of the anal fin, body markings, shape of the mouth and distribution of the tubercles indicate that this species belongs to *Opsaridium*. Matthes (1965) discussed the likely affinity of *B. leleupi* with *O. zambesense* and *B. boweni* Fowler, 1930; the latter species he considered might be synonymous with *O. zambesense*.

Barilius engrauloides Nichols, 1923. Described from a single specimen collected from the Ubangui river. In his description Nichols states '. . . It seems to be more or less intermediate between species of that genus (*Barilius*) and of *Engraulicypris*'. The figure accompanying the description is crudely drawn and of no help in determining the generic allocation of this species.

RAIAMAS Jordan, 1919

Barilius (non Hamilton), Boulenger, 1899 (part).
Bola Günther, 1868.
Sagittabarilius Fowler, 1936.

Type species: *Cyprinus bola* Hamilton, 1822.

Distribution: Africa, Nilotic, Guinean and Zairean ichthyofaunal provinces (see Roberts, 1975 for definition of these provinces); northern India; Burma and the Malay Peninsula.

Günther (1868) first recognized a generic separation for *Barilius bola* and used the generic name *Bola*. However, this name was preoccupied and the name *Raiamas* was proposed as a replacement by Jordan (1919).

Hora & Mukerji (1936) accepted Jordan's substitute name but later, Hora (1937) discussed the nomenclatural history of *Barilius bola* and decided that *Raiamas* had been proposed in error because the name *Opsarius* McClelland, 1839 was available. Hora's (1937) contention was that Day (1869) had restricted the use of *Opsarius* McClelland to *Barilius bola*. Day had, however, simply placed *B. bola* in the genus *Opsarius* without designating it as the type of that genus, and later (1889) he included *Opsarius* in the synonymy of *Barilius*. McClelland (1839) had not designated a type species for the genus *Opsarius*, an action subsequently taken by Jordan (1919) who selected the species *maculatus* on the grounds of logotypy. *Opsarius maculatus* is a synonym of *Barilius tilheo* (Hamilton, 1822).

Smith (1945) used Jordan's name *Raiamas* for *bola* although his reasons for justifying its generic allocation, i.e. on the basis of its pharyngeal dentition, are not those used here. Smith (1945) stated that the two rows of pharyngeal teeth in *R. bola* distinguish it from all other *Barilius*, which have three rows. In all specimens of *R. bola* I have examined there are three rows, a feature also noted and illustrated by Hora (1937).

Included African species: *R. ansorgii* (Blgr, 1910), *R. batesii* (Blgr, 1914), *R. buchholzi* (Peters, 1876), see comments below, *R. kingsleyae* (Blgr, 1899), see comments below, *R. loati* (Blgr, 1909), see comments below, *R. nigeriensis* (Daget, 1951), *R. salmolucius* (Nichols & Griscom, 1917), *R. silax* (Schultz, 1942), *R. senegalensis* (Steind., 1870), *R. steindachneri* (Pell., 1908), *R. longirostris* (Blgr, 1902), see comments below, *R. macrostoma* (Blgr, 1913), *R. moorii* (Blgr, 1900), *R. weeksi* (Blgr, 1899), *R. shariensis* (Fowler, 1949).

Raiamas buchholzi (Peters)

Of this species, Boulenger (1911) stated that it was separable from *Barilius kingsleyae* only on the number of lateral line scales (46 cf. 49–51 according to Boulenger) and '. . . may ultimately have to be regarded as not separable from it'. Although I have not had the opportunity to see the type specimen of *R. buchholzi* it is clear from Peters' (1876) illustration that it should be included in *Raiamas*. In *R. kingsleyae* the number of lateral line scales ranges from 46 to 49 (51 only if counting onto the caudal fin). I find no other differences between *R. kingsleyae* and Peters' description of *R. buchholzi* apart from the apparent lack of body markings in the latter (faint vertical bars are present in *R. kingsleyae* but are lacking in some specimens, no doubt due to the effects of preservation). I therefore propose that *Raiamas kingsleyae* be regarded as a junior synonym of *Raiamas buchholzi*.

Raiamas longirostris (Blgr)

Known only from the holotype collected at Ubanghi, this species was placed by Fowler (1936) in the subgenus *Sagittabarilius* along with *R. salmolucius*. The principal features Fowler used to characterize *Sagittabarilius* were the slender body, long maxilla and wide infraorbitals – characters shared by all *Raiamas* species.

Dr K. E. Banister has examined the holotype in Tervuren Museum and reports that the characteristic elongate snout is not an artefact and in this regard *R. longirostris* closely resembles *R. bola* (see below).

Raiamas loati (Blgr) group

The complex of species represented by *R. loati* in the east, *R. salmolucius* in the west and by *R. ansorgii* in the south-west appears to be a morphoclinal series of taxa. If the descriptions of the west African species given by Boulenger (1911, 1916) are compared closely, the only differences to be found are in lateral line scale counts and some body proportions.

Raiamas loati is readily distinguished from the west and south-western species complex by its long maxilla (extending to the posterior third of the orbit), elongate pectoral and pelvic axial fin lobes (half the length of their respective fins), length and shape of the 1st infraorbital bone (equal to eye diameter and with the upper posterior edge slightly extended along the 2nd infraorbital).

In contrast *R. senegalensis*, *R. steindachneri*, *R. buchholzi* and *R. ansorgii* all have a relatively short maxilla, short pectoral and pelvic axial fin lobes, and a short 1st infraorbital bone – the upper border of which extends posteriorly as a narrow triangle.

Regarding *R. macrostoma*, Boulenger (1916) noted '... Intermediate between *B. loati* and *B. senegalensis*'. Its elongate axial fin lobes and shape of the 1st infraorbital bone suggest that it is more closely allied to *R. loati*.

Even within the relatively small number of specimens of the west African species examined, 'intermediates' between all species can be found.

Two Asian species are included in *Raiamas*, *R. bola* (Hamilton, 1822) and *R. guttatus* (Day, 1869). These species are almost identical in cranial morphology but differ in certain other characters. The lateral line scales in *R. bola* number 88–94 but 44–48 in *R. guttatus*. Barbels are absent in *R. bola* but in *R. guttatus* there are two minute posterior maxillary barbels. Smith (1945) says of *R. bola* that its 'scales are finer than any known species of *Barilius*'. However, they compare in shape and striation with those of other *Raiamas*, *Opsaridium* and *Barilius* species. According to Hora & Mukerji (1936) *R. bola* is confined to the hilly areas of the Northwest Provinces of India, Assam, Bengal, Orissa and Burma. Fowler (1934) records the species from Thailand but appears to have mistaken *R. guttatus* for *R. bola* (see Smith, 1945). *Raiamas guttatus* occurs in the Shan States, Burma, Thailand, Cambodia (Khmer Republic) and the Malay Peninsula.

LUCIOSOMA Bleeker, 1855

TYPE SPECIES: *Barbus setigerus* Valenciennes, 1842.

DISTRIBUTION: Thailand, Java, Sumatra, Borneo and Laos.

The following species are included in the genus: *L. setigerum* (Val., 1842); *L. spilopleura* Bleeker, 1865; *L. bleekeri* Steind., 1879; *L. trinema* Bleeker, 1852; *L. pellegrini* Popta, 1905.

Luciosoma fasciata Yang & Hwang, 1964 appears from the figure not to belong to this genus. The shape of the head and mouth, the position of the dorsal fin, length of the pectoral fin, and the high number of lateral line scales all indicate a species of *Raiamas*, possibly *R. guttatus*.

PARLUCIOSOMA Howes, 1980

TYPE SPECIES: *Leuciscus argyrotaenia* Bleeker, 1850.

DISTRIBUTION: India, Thailand, Malay peninsula and Sunda Islands.

Included species: *P. argyrotaenia* (Bleeker, 1850), *P. dusonensis* (Bleeker, 1851), *P. daniconius* (Hamilton, 1822), *P. cephalotaenia* (Bleeker, 1859), *P. volzi* (Popta, 1905).

Species descriptions and details of their distribution are given by Brittan (1954). Species which probably belong to this genus, but which I have not had the opportunity of examining, are: *Rasbora steineri* Nichols & Pope, 1927, *R. hubbsi* Brittan, 1954, *R. myersi* Brittan, 1954, *R. tawarensis* Weber & de Beaufort, 1916.

Mention may be made at this point of *Rasbora zanzibarensis* Günther, 1866 reportedly collected from the Rovuma river, East Africa, and to date the only known representative of the genus in Africa. Day (1877) placed the species in the synonymy of *Rasbora daniconius*, an action followed by Brittan (1954). Neither author made particular mention of the African locality of the species. I have examined the unique type of *R. zanzibarensis* and find that it is a *Rasbora*, but I am doubtful that it belongs to the species *daniconius*. I also doubt the provenance of the fish is Africa and I suspect that there has been an error concerning the locality citation. For the present *R. zanzibarensis* must remain a *species inquirendum*.

MEGARASBORA Günther, 1868

TYPE AND ONLY KNOWN SPECIES: *Cyprinus elanga* Hamilton, 1822.

DISTRIBUTION: Bengal, Assam and western Burma.

The species has been described by Brittan (1954) and an osteological description is given above, p. 183.

Appendix 2

A note on the taxa formerly included in Engraulicypris

As *Engraulicypris* is now restricted to the type species, *E. sardella* (see p. 182), the species previously included must be referred to another genus. A preliminary review of the anatomy of these species has indicated on the basis of synapomorphic characters that they belong to three genera, namely *Neobola*, *Rastrineobola* and *Chelaethiops*. The apomorph characters defining the genera and their contained species are as follows:

NEOBOLA Vinciguerra, 1895

TYPE SPECIES: *Neobola bottegi* Vinciguerra, 1895.

APOMORPH CHARACTERS: Deep, narrow ethmoid block, the dorsal surface (supraethmoid) channelled, elongate nasal, raised frontal sensory canal, narrow infraorbitals, separation of the dermo- and autopterotic by a posttemporal fossa, long anterior premaxillary processes, attenuated opercular border, rounded anterior articular face of 1st vertebra.
INCLUDED SPECIES: *N. bottegi* Vinc., 1895, *N. fluviatilis* (Whitehead, 1962), *N. brevianalis* (Blgr, 1908), *N. bredoi* (Poll, 1945), *N. spinifer* (Bailey & Matthes, 1971), *N. stellae* (Worthington, 1934), *N. moeurensis* (Blgr., 1915).

RASTRINEOBOLA Fowler, 1934

TYPE SPECIES: *Neobola argentea* Pellegrin, 1904.

APOMORPH CHARACTERS: Long, ventrally directed medial maxillary processes, long post-coronoid dentary border.

INCLUDED SPECIES: *R. argentea* (Pellegrin, 1904).

CHELAETHIOPS Boulenger, 1899

TYPE SPECIES: *Chelaethiops elongatus* Blgr, 1899.

APOMORPH CHARACTERS: Supraethmoid narrow, channelled and overlapped by the frontals, raised frontal sensory canal, elongate jaws, maxillaries contacting one another medially, separation of the dermo- and autopterotic by a posttemporal fossa, anterior articular face of 1st vertebra rounded with caudally directed lateral processes, elongate pectoral axial scale, numerous olfactory lamellae. In addition the jaw musculature shows derived features.

INCLUDED SPECIES: *C. elongatus* Blgr, 1899, *C. bibie* (Joannis, 1835), *C. congicus* (Nichols & Griscom, 1917), *C. minutus* (Blgr, 1906).

I have examined the type specimens of both *Chelaethiops congicus* and *C. katangae* Poll, 1948, and it is my opinion that the latter is a synonym of the former. Specimens catalogued in the BM(NH) collections as *C. congicus* are not this species and represent an undescribed taxon (or taxa). Ricardo (1939) described from Lake Rukwa a subspecies of *C. congicus*. However, her description was based on the examination of the misidentified comparative material noted above. Although *rukwaensis* is indeed a discrete taxon it is not closely related to *C. congicus*, although it is related to the undescribed taxa from Lake Tanganyika and the Malagarasi river. Thus, Ricardo's subspecies is here recognized as a species, *Chelaethiops rukwaensis* Ricardo, 1939.

The relationships of *Neobola*, *Rastrineobola* and *Chelaethiops* remain to be investigated, but my preliminary observations indicate that all three genera form a monophyletic assemblage related to middle Asian and European groups as represented by *Phoxinellus* (of which there are two African species, *P. chaignoni* and *P. callensis*). There is thus no close relationship with the bariliine group.

References

Bănărescu, P. 1968. Revision of the genera *Zacco* & *Opsariichthys* (Pisces, Cyprinidae). *Věst. čsl. zool. Spol* **32** (4) : 305–210.

Banister, K. E. & Clarke, M. A. 1977. The freshwater fishes of the Arabian Peninsula. In: The scientific results of the Oman flora and fauna survey 1975. *Jl. Oman Stud.* **2** : 111–154.

—— —— In press. A revision of the large *Barbus* of Lake Malawi with a reconstruction of the history of the southern Rift Valley lakes. *J. nat. Hist.*

Berg, L. S. 1964. *Freshwater fishes of the USSR and adjacent countries*. **2**. (English translation of the fourth ed. of 1949.) 496 pp.

Bleeker, P. 1859. Conspectus systematis Cyprinorum. *Natuurk Tijdschr. Ned.-Indië* **20** : 421–441.

—— 1863. *Atlas ichthologique des Indes Orientales Needlandaises*. Cyprins **3**. Amsterdam : 1–150.

Boulenger, G. A. 1911. *Catalogue of African freshwater fishes in the British Museum* (*Natural History*) **2** : 529 pp.

—— 1916. *Catalogue of African freshwater fishes in the British Museum* (*Natural History*) **4** : 392 pp.

Briggs, J. C. 1979. Ostariophysan Zoogeography: an alternative hypothesis. *Copeia* **1979** (1) : 111–118.

Brittan, M. R. 1954. *A revision of the Indo-Malayan fresh-water fish genus Rasbora*. Institute of Science & Technology, Manila. 224 pp.

Brousseau, R. A. 1976. The pectoral anatomy of selected Ostariophysi. II. The Cypriniformes and siluriformes. *J. Morph.* **150** : 79–115.

Burton, C. K. 1970. The palaeotectonic status of the Malay Peninsula. *Palaeogeogr. Palaeoclimat. Palaeoecol.* **7** : 51–60.

Chu, Y. T. 1935. Comparative studies on the scales and on the pharyngeals and their teeth in Chinese cyprinids, with particular reference to taxonomy and evolution. *Biol. Bull. St. John's Univ., Shanghai* **2** : 1–225.

Daget, J. 1962. Les poissons du Fouta Dialon et de las basse Guinée. *Mem. Inst. fr. Afr. noire* **65** : 1–210.

Day, F. 1869. On the fishes of Orissa. *Proc. zool. Soc. Lond.* : 369–387.

—— 1877. *The fishes of India* Pt. III : 369–552. London.

—— 1889. *The fauna of British India, including Ceylon and Burma*. Fishes **1**. London, 548 pp.

Evans, H. M. 1940. *Brain and body of fish*. London. 164 pp.

Forey, P. L. 1975. A fossil clupeomorph fish from the Albian of the Northwest Territories of Canada, with notes on cladistic relationships of clupeomorphs. *J. Zool., Lond.* **175** : 151–177.

Fowler, H. W. 1934. Zoological results of the third de Schaunensee Siamese Expedition Part 1. Fishes. *Proc. Acad. nat. Sci. Philad.* **86** : 67–163.

—— 1936. Zoological results of the George Vanderbilt Africa expedition of 1934. Part III. The freshwater fishes. *Proc. Acad. nat. Sci. Philad.* **88** : 243–335.

Gilbert, C. R. & Bailey, R. M. 1972. Systematics and zoogeograply of the American cyprinid fish *Notropis* (*Opsopoedus*) *emiliae*. *Occ. Pap. Mus. Zool. Univ. Mich.* **664** : 1–35.

Goren, M., Fishelson, L. & Trewavas, E. 1973. The cyprinid fishes of *Acanthobrama* Heckel and related genera. *Bull. Brit. Mus. nat. Hist.* (Zool.) **24** (6) : 293–315.

Gosline, W. A. 1978. Unbranched dorsal-fin rays and subfamily classification in the fish family Cyprinidae. *Occ. Pap. Mus. Zool. Univ. Mich.* **684** : 1–21.

Gosse, J.-P. 1966. Remarques systématiques sur quelques espèces de la faune ichthyologique congolaise. *Revue Zool. Bot. afr.* **73** (1–2) : 186–200.

Greenwood, P. H. 1976. A review of the family Centropomidae (Pisces, Perciformes). *Bull. Brit. Mus. nat. Hist.* (Zool.) **29** (1) : 1–81.

——**, Rosen, D. E., Weitzman, S. H. & Myers, G. S.** 1966. Phyletic studies of teleostean fishes, with a provisional classification of living forms. *Bull. Am. Mus. nat. Hist.* **131** : 339–456.

Günther, A. 1864. Report on a collection of fishes made by Dr Kirk in the Zambesi and Nyassa Regions. *Proc. zool. Soc. Lond.* : 303–314.

—— 1868. *Catalogue of fishes in the British Museum.* **7** : 1–512.

Hamilton, F. 1822. *An account of the fishes found in the River Ganges and its branches.* Edinburgh, 405 pp.

Heckel, J. J. 1842. Ichthyologie (von Syrien). In: Russeggar, J. V. *Reisen in Europa, Asien* und *Africa* etc. Pt. 1 : 993–1099.

Hora, S. L. 1921. Fish and fisheries of Manipur with some observations on those of the Naga Hills. *Rec. Ind. Mus.* **22** : 165–214.

—— 1937. The game fishes of India. *J. Bombay Nat. Hist. Soc.* **39** : 199–210.

—— **& Mukerji, U. D.** 1936. Fish of the Eastern Doons, United Provinces. *Rec. Ind. Mus.* **38** (2) : 133–146.

Howes, G. J. 1978. The anatomy and relationships of the cyprinid fish *Luciobrama macrocephalus* (Lacepède). *Bull. Br. Mus. nat. Hist.* (Zool.) **34** (1) : 1–64.

—— 1979. Notes on the anatomy of the cyprinid fish *Macrochirichthys macrochirus* with a review of the subfamily Cultrinae. *Bull. Br. Mus. nat. Hist.* (Zool.) **36** (3) : 147–200.

Jordan, D. S. 1919. *The genera of fishes*, Part 3. Leland Stanford Junior Univ. Pubs, University Series : 285–410 + i–xv.

—— **& Richardson, R. E.** 1909. A catalog of the fishes of the island of Formosa, or Taiwan, based on the collections of Dr Hans Sauter. *Mem. Carnegie Mus.* **4** (4) : 159–204.

Jubb, R. A. 1967. *Freshwater fishes of Southern Africa.* Cape Town. 24 pp.

McClelland, J. 1839. Indian Cyprinidae *Asiat. Reschs* **19** (2) : 217–471.

Matthes, H. 1963. A comparative study of the feeding mechanism of some African Cyprinidae (Pisces, Cypriniformes). *Bijdr. Dierk.* **33** : 3–35.

—— 1965. Quelques poissons nouveaux du Congo. *Revue Zool. Bot. afr.* **71** : 177–193.

Menon, A. G. K. 1951. Further studies regarding Hora's Satpura hypothesis. *Proc. natn. Inst. Sci. India* **17** (6) : 475–497.

—— 1953. Age of transgression of the bay of Bengal and its significance in the evolution of the freshwater fish fauna of India. *Bull. natn. Inst. Sci. India* **7** : 240–247.

—— 1955. The external relationships of the Indian freshwater fishes, with special reference to the countries bordering the Indian ocean. *J. Asiatic Soc. Calcutta* **21** (1) : 31–38.

Mirza, M. R. 1974. Freshwater fishes and ichthyogeography of Baluchistan and adjoining areas of the Indus plain, Pakistan. *Biologia* **20** (1) : 67–82.

Nakamura, M. 1969. *Cyprinid fishes of Japan.* Tokyo. 451 pp.

Nichols, J. T. 1923. New African fishes. *Amer. Mus. Novit.* **57** : 1–3.

—— 1943. *Freshwater fishes of China.* Nat. Hist. of Central Asia **9**. Amer. Mus. of Nat. Hist., N.Y. 322 pp.

Nieuwenhuys, R. 1962. Trends in the evolution of the Actinopterygian forebrain. .*J Morph.* **111** : 69–88.

Norman, J. R. 1922. Four new fishes from Tanganyika Territory. *Ann. Mag. nat. Hist.* (9) **9** : 686–688.

Okada, Y. 1960. Studies on the freshwater fishes of Japan. II. Special Part. *J. Fac. Fish. pref. Univ. Mie-Tsu* **4** (2) : 267–588.

Patterson, C. 1975. The braincase of pholidophorid and leptolepid fishes, with a review of the actinopterygian braincase. *Phil. Trans. Roy. Soc.* **B 269** (899) : 275–579.

Pellegrin, J. 1926. Description d'un Cyprinidé nouveau récolté au Congo Belge par le Dr Schouteden. *Revue Zool. Bot. afr.* **14** : 40–41.

Peters, W. C. H. 1876. Uber die von Professor Dr. Reinhold Buchholz in Westafrica gesammelten Fische. *Mber. dt. Akad. Wiss. Berl.* : 244–252.

Poll, M. 1953. Poissons non Cichlidae. *Result. scient. Explor. hydrobiol. Lac Tanganyika* (1946–1947) **3** (5A) : 1–251.

—— 1967. Contribution à la faune ichthyologique de l'Angola. *Publicoes cult. Co. Diam. Angola* no. **75** : 1–381.

—— **& Gosse, J.-P.** 1963. Contribution à l'étude systématique de la faune ichthyologique du Congo Central. *Ann. Mus. roy. Afr. Cent.* Zool. **116** : 43–111.

Ramaswami, L. S. 1955. Skeleton of cyprinoid fishes in relation to phylogenetic studies: 7. The skull and Weberian apparatus of the Cyprininae (Cyprinidae). *Acta Zool.* **36** (3) : 199–242.

Regan, C. T. 1908. Description of new fishes from Lake Candidus, Formosa, collected by Dr A. Moltrecth. *Ann. Mag. nat. Hist.* (8) **2** : 358–360.

—— 1911. The classification of the teleostean fishes of the order Ostariophysi. 1. Cyprinoidei. *Ann. Mag. nat. Hist.* (8) **8** : 13–32.

—— 1922. The distribution of the fishes of the order Ostariophysi. *Bijdr. Dierk.* **22** : 203–207.

Ricardo, C. K. 1939. The fishes of Lake Rukwa. *J. Linn. Soc.* (Zool.) **40** (275) : 625–657.

Ridd, M. F. 1971. South-East Asia as a part of Gondwanaland. *Nature, Lond.* **230** : 531–533.

Roberts, T. R. 1973. Interrelationships of ostariophysans. *In*: *Interrelationships of fishes.* Greenwood, P. H., Miles, R. S. & Patterson, C. (Eds) : 373–395. London and New York.

—— 1975. Geographical distribution of African freshwater fishes. *Zool. J. Linn. Soc.* **57** (4) : 249–319.

Rognes, K. 1973. Head skeleton and jaw mechanism in Labrinae (Teleostei : Labridae) from Norwegian waters. *Arbok Univ. Bergen Mat.-Naturv.* Ser. no. 4 : 1–149.

Schnitzlein, H. N. 1964. Correlation of habit and structure in the fish brain. *Amer. Zool.* **4** : 21–32.

Seggar, J. 1961. Telencephalon and behaviour in *Gasterosteus aculeatus. Behaviour* **18** : 256–287.

Silas, E. G. 1955. Speciation among the freshwater fishes of Ceylon. *Bull. natn. Inst. Sci. India* **7** : 248–259.

Smith, H. W. 1945. The fresh-water fishes of Siam, or Thailand. *Bull. U.S. natn Mus.* **188** : 1–622.

Stauffer, P. H. 1974. Malaya and southeast Asia in the pattern of continental drift. *Bull. geol. Soc. Malaysia* **7** : 89–138.

Tretiakov, D. K. 1946. Systematic groups of Cyprinidae. *Zool. Zh.* **25** (2) : 149–156.

Vandewalle, P. 1974. On the anatomy and function of the head region in *Gobio gobio* (L.) (Pisces, Cyprinidae). 2. The trigemino-facialis chamber and some adjacent structures. *Forma Functio* **7** : 119–124.

Verraes, W. 1974. Discussion on some functional–morphological relations between some parts of the chondrocranium and the osteocranium in the skull base and the skull roof, and of some soft head parts during postembryonic development of Salmo gairdneri Richardson 1836 (Teleostei : Salmonidae). *Forma Functio* **7** : 281–292.

Yang, Y-J. & Hwang, H.-C. 1964. Leuciscinae. *In*: Wu, H.-W. *Cyprinid fishes of China* **1**. Shanghai. 228 pp.

Weitzman, S. 1962. The osteology of *Brycon meeki*, a generalized characin fish, with an osteological definition of the family. *Stanford ichthyol. Bull.* **8** (1) : 3–77.

Wiley, M. L. & Collette, B. B. 1970. Breeding tubercles and contact organs in fishes: their occurrence, structure and significance. *Bull. Am. Mus. nat. Hist.* **143** art. 3 : 143–216.

Worthington, E. B. & Ricardo, C. K. 1936. The fish of Lake Tanganyika (other than Cichlidae). *Proc. zool. Soc. Lond.* (4) : 1061–1112.

Wu, Hsien-Wen, 1964. *Cyprinid fishes of China* **1**. Shanghai. 228 pp.

Manuscript accepted for publication 28 March 1979

British Museum (Natural History)
Publication on fishes

The Cichlid fishes of Lake Victoria, East Africa. The biology and evolution of a species flock. P. H. Greenwood.
Bull. British Museum (Natural History) Zool. Suppl. No. 6, 1974
vi + 134 pp, 1 coloured plate, 77 text figures, 4to, (paper) £6.00
(boards) £8.25

The feeding mechanisms of a deep sea fish, Chauliodus sloani Schneider. V. V. Tchernavin
1953, viii + 101 pp, 10 plates, 36 text figures, 4to paper, £3.85

Forty drawings of fishes, made by the artists who accompanied Captain James Cook. P. J. P. Whitehead
1968, xxvii pp. 36 collotype colour plates, demy folio boards, £55.00

The Clupeoid fishes described by Lacepede, Cuvier and Valenciennes. P. J. P. Whitehead
Bull. British Museum (Natural History) Zool. Suppl. No. 2, 1967,
180 pp, 11 plates, 15 text figures, 4to paper, £7.00

The Clupeoid fishes of the Guianas. P. J. P. Whitehead
Bull. British Museum (Natural History) Zool. Suppl. No. 5, 1973,
227 pp, 72 text figures, 6 tables, 4to paper, £13.50

Titles to be published in Volume 37

Miscellanea

The echinoderms of Aldabra and their habitats. By N. A. Sloan, Ailsa M. Clark & J. D. Taylor

The anatomy, phylogeny and classification of bariliine cyprinid fishes. By G. J. Howes

The Fellodistomidae (Digenea) of fishes from the northeast Atlantic. By Rodney A. Bray & David L. Gibson

Printed by Henry Ling Ltd, Dorchester

Bulletin of the
British Museum (Natural History)

The Fellodistomidae (Digenea) of fishes from the northeast Atlantic

Rodney A. Bray & David I. Gibson

Zoology series Vol 37 No 4 28 February 1980

The *Bulletin of the British Museum* (*Natural History*), instituted in 1949, is issued in four scientific series, Botany, Entomology, Geology (incorporating Mineralogy) and Zoology, and an Historical series.

Papers in the *Bulletin* are primarily the results of research carried out on the unique and ever-growing collections of the Museum, both by the scientific staff of the Museum and by specialists from elsewhere who make use of the Museum's resources. Many of the papers are works of reference that will remain indispensable for years to come.

Parts are published at irregular intervals as they become ready, each is complete in itself, available separately, and individually priced. Volumes contain about 300 pages and are not necessarily completed within one calendar year. Subscriptions may be placed for one or more series. Subscriptions vary according to the contents of the Volume and are based on a forecast list of titles. As each Volume nears completion, subscribers are informed of the cost of the next Volume and invited to renew their subscriptions. Orders and enquiries should be sent to:

Publications Sales,
British Museum (Natural History),
Cromwell Road,
London SW7 5BD,
England

World List abbreviation: *Bull. Br. Mus. nat. Hist.* (Zool.)

© Trustees of the British Museum (Natural History), 1980

This number completes Volume 37

ISSN 0007-1498

British Museum (Natural History)
Cromwell Road
London SW7 5BD

Zoology series
Vol 37 No 4 pp 199-293

Issued 28 February 1980

GENERAL
29 FEB 19
LIBRARY
NATURAL HIS

The Fellodistomidae (Digenea) of fishes from the northeast Atlantic

Rodney A. Bray & David I. Gibson
k
Department of Zoology, British Museum (Natural History), Cromwell Road, London SW7 5BD

Contents

Introduction . . . 199
Materials and methods . . . 199
Systematic section . . . 200
  Family Fellodistomidae . . . 200
    A taxonomic history of the group . . . 200
    Some comments on forms previously treated as fellodistomids . . . 201
    Aspects of biology . . . 202
   Subfamily Fellodistominae . . . 202
    Fellodistomum fellis . . . 205
    Steringophorus furciger . . . 212
    Steringophorus agnotus . . . 217
    Steringophorus blackeri . . . 220
    Steringophorus pritchardae . . . 223
    Steringophorus thulini . . . 226
    Olssonium turneri . . . 229
    Steringotrema pagelli . . . 234
    Steringotrema divergens . . . 239
    Steringotrema ovacutum . . . 242
    Prudhoeus nicholsi . . . 245
   Subfamily Baccigerinae . . . 248
    Bacciger bacciger . . . 250
    Pronoprymna ventricosa . . . 255
   Subfamily Xenoperinae . . . 259
    Proctoeces maculatus . . . 262
   Subfamily Monascinae . . . 268
    Monascus filiformis . . . 268
   Subfamily Tergestiinae . . . 274
    Tergestia laticollis . . . 276
Host–parasite list . . . 281
Acknowledgements . . . 282
References . . . 283

Introduction

This is the third in a projected series of papers on the helminth-fauna of fishes from the northeast Atlantic region. The family discussed is the Fellodistomidae, a group restricted mainly to marine fishes, but occurring occasionally in freshwater fishes and as adults in marine invertebrates.

Materials and methods

The materials and methods used in this investigation are outlined in the first two papers in this series (Bray & Gibson, 1977; Gibson & Bray, 1977). In addition to the sources of material mentioned in these two papers, we have collected further material at Aberdeen in March–April 1977, and aboard MAFF RV *Cirolana* in NE Atlantic in 1978. In this report we have used the nomenclature and classification of fishes presented by Hureau & Monod (1973).

Bull. Br. Mus. nat. Hist. (Zool.) **37** (4) : 199–293   Issued 28 February 1980

Systematic section

Family **FELLODISTOMIDAE** Nicoll, 1909

Steringophoridae Odhner, 1911.
Xenoperidae Poche, 1926.
Monascidae Dollfus, 1947.

DIAGNOSTIC FEATURES. Body large to small; globular to elongate. Body-surface usually smooth; occasionally bearing spines or muscular ornamentation. Oral sucker subterminal; globular. Ventral sucker globular; large to small; in middle or anterior half of body. Prepharynx short to apparently absent. Pharynx well developed; globular to elongate. Oesophagus absent to long. Gut-caeca normally two; narrow to wide; reaching to testes or beyond; occasionally with single caecum (? opening into excretory vesicle). Testes two; oval to globular; entire or deeply lobed; symmetrical, oblique or tandem; in anterior or posterior hindbody; normally post-ovarian. Cirrus-sac usually well developed, occasionally absent; oval to claviform; containing seminal vesicle, pars prostatica, prostatic cells and ejaculatory duct. Seminal vesicle usually bipartite; occasionally globular or convoluted and tubular. Pars prostatica usually wide with filamentous lining; occasionally greatly reduced. Spermatophores may be produced. Ejaculatory duct usually wide and convoluted; occasionally small and narrow. Genital atrium short to long. Genital pore ventral; usually sinistral; in middle or posterior half of forebody. Ovary entire to multilobate; in hindbody; usually anterior to testes. Laurer's canal present. Uterine seminal receptacle usually present; canalicular seminal receptacle (see Gibson & Bray, 1979) occasionally present. Uterus normally reaching posteriorly to testes; bulk of uterus usually post-testicular. Eggs numerous; small; variable; operculate; egg-shell occasionally ornamented. Vitellarium follicular; typically in two lateral fields; occasionally amalgamated to form two oval masses; occasionally confluent medially. Excretory pore terminal; vesicle 'Y'- or 'V'-shaped, with anterior arms reaching to about level of pharynx. Parasitic in intestine, pyloric caeca, bile duct and gall-bladder of marine, and occasionally freshwater, teleosts; occasionally occurring as adults in molluscs (bivalves and gastropods).

A taxonomic history of the group

Nicoll (1909*a*) erected the subfamily Fellodistominae in the suborder Prosostomata Odhner, 1905, to include the two genera *Fellodistomum* Stafford, 1904, and *Steringophorus* Odhner, 1905. Two years later Odhner (1911*a*), in erecting the new family Steringophoridae, provided the first detailed concept of this group. In it he included *Steringophorus*, *Fellodistomum*, *Tergestia* Stossich, 1899, and four new genera, *Rhodotrema*, *Steringotrema*, *Haplocladus* and *Proctoeces*. The name Steringophorinae was used by Odhner to replace the name Fellodistominae, as he felt that it was more appropriate and, in addition to *Steringophorus* and *Fellodistomum*, he included *Rhodotrema* and *Steringotrema*. For the remaining genera, *Haplocladus*, *Proctoeces* and *Tergestia*, he erected the subfamily Haplocladinae. Woodcock (1912) first used the name Fellodistomidae, and Nicoll (1913) pointed out its priority to the appellation Steringophoridae.

The two subfamilies Steringophorinae [=Fellodistominae] and Haplocladinae were recognized by Fuhrmann (1928) and Issaitschikov (1928), the Steringophorinae having grown to include six genera and the Haplocladinae to include four genera. The next important developments were made by Dollfus (1952), who recognized four subfamilies, the Fellodistomatinae [*sic*], containing four genera with a pre-testicular uterus, the Steringophorinae, containing 14 genera with the uterus mainly post-testicular, the Monascinae Dollfus, 1947, containing five genera with the uterus distributed both anteriorly and posteriorly to the testes, and the Discogasteroidinae Srivastava, 1939, containing two genera with a number of characteristics including short caeca and a seminal receptacle. Cable (1953), using evidence from life-history studies, included the Fellodistominae, Haplocladinae, Tandanicolinae Johnston, 1927, and Gymnophallinae Odhner, 1905, in the Fellodistomatidae [*sic*]; but Yamaguti (1953*a*), although including 20 genera in the family, did not recognize any of the subfamilies. Skrjabin & Koval (1957), however, further subdivided the family into 11 subfamilies, the Fellodistomatinae [*sic*], the Discogasteroidinae, the

Haplocladinae, and eight new subfamilies, the Ancylocoeliinae, the Antorchiinae, the Lissolomatinae, the Markevitschiellinae, the Pyriformiinae, the Proctoecinae, the Tergestiinae and the Yamagutiinae. Yamaguti (1958) recognized 10 subfamilies, the Fellodistominae, the Monascinae, the Discogasteroidinae, the Antorchiinae, the Pyriforminae, the Tergestiinae, the Lissolomatinae, the Heterorchiinae Dollfus, 1950, and two new subfamilies, the Pentagramminae and the Symmetrovesiculinae [being unaware of Skrjabin & Koval's (1957) work, Yamaguti also considered that four of the other subfamilies were new]. Baer & Joyeux (1961), however, retained only four subfamilies, the Fellodistomatinae [*sic*], the Antorchiinae, the Gymnophallinae and the Heterorchiinae. Mehra (1963) recognized 9 subfamilies, synonymizing the Discogasteroidinae with the Fellodistominae and the Pentagramminae with the Antorchiinae. He also included the Baccigerinae Yamaguti, 1958, transferring it from the Cryptogonimidae Ward, 1917. Overstreet (1969) and Angel (1971) considered the Monodhelminthinae Dollfus, 1937, as a subfamily of the Fellodistomidae and, finally, Yamaguti (1971) recognized 15 subfamilies, the Baccigerinae, Proctoecinae, Parantorchiinae Yamaguti, 1958, Lintoniinae Yamaguti, 1970, Stenakrinae Yamaguti, 1970, and two new subfamilies, the Trigonocryptinae and the Infundibulostominae, being added to his earlier (1958) list. Yamaguti (1971) followed Travassos, Teixeira de Freitas & Bührnheim (1965) in giving family-status to the Monascinae and considered the Pentagramminae to be synonymous with the Baccigerinae.

It can safely be said that not since the work of Odhner (1911*a*) has a revision of the family been solidly based on a study of specimens of the genera involved. As can be seen from the brief summary presented above, much juggling of the subfamilies has occurred during the history of this family. This is not the place to attempt a complete reclassification of the group, being beyond the scope of this series. A detailed study of those forms from the northeast Atlantic region has, however, been undertaken. The following five subfamilies are, therefore, considered here: the Fellodistominae, the Baccigerinae, the Xenoperinae Poche, 1926, the Tergestiinae and the Monascinae.

Some comments on forms previously treated as fellodistomids

Certain genera, which at one time or another have been considered as fellodistomids, have been omitted from this study. *Ancylocoelium* Nicoll, 1912, was originally included in the Haplocladinae; but Nicoll indicated that its relationships are not straightforward and that its designation was provisional. In our opinion, its most satisfactory position is in the Monorchiidae Odhner, 1911. A close comparison of this genus with *Chrisomon tropicus* (Manter, 1940) as described by Kovaleva (1970*a*) from the same host may reveal that Nicoll (1912) misinterpreted certain features.

The Stenakrinae was included in the Fellodistomidae by Yamaguti (1970, 1971); but an examination of members of this subfamily has led us to believe that it is best placed in the Opecoelidae Ozaki, 1925. *Stenakron* Stafford, 1904, was not well known until studied by the Russian workers Strelkov (1960) and Mamaev, Parukhin & Baeva (1963). Prior to the latter work this genus was always considered an allocreadiid, but Mamaev *et al.* placed it in the Fellodistomidae. It has been confused with *Rhodotrema* Odhner, 1911, particularly by Russian workers: this confusion is discussed below (p. 245). Having studied *Stenakron vetustum* Stafford, 1904, *S. kerguelense* Prudhoe & Bray, 1973, *Anisorchis opisthorchis* Polyanski, 1955, and *Caudotestis nicolli* Issaitschikov, 1928, Bray (1979) was able to point out that the members of this subfamily differ from the Fellodistomidae in the following characters: I-shaped excretory vesicle; long claviform cirrus-sac containing single large sac-like seminal vesicle; small narrow pars prostatica; and long ejaculatory duct. Other normal characters of the Stenakrinae are unusual in the Fellodistomidae: these include large eggs, a pre-testicular uterus and vitelline fields confluent in the median line. It is also possible that the cercariae of *Stenakron* are microcercous and occur in gastropods, as in the case of the opecoelids; but the cercariae apparently lack a stylet (Chubrik, 1966). Gaevskaja & Kovaleva (1977) follow Prudhoe & Bray (1973) in including *Stenakron* in the Opecoelidae.

Another putative member of the Fellodistomidae is *Yamagutia anarhichae* Brinkmann, 1956, from the gall-bladder of *Anarhichas minor* from Iceland. This taxon is based upon a single well-flattened specimen, which, through the kindness of Dr F. Gudmundsson of the Museum of Natural History, Reykjavik, we have been able to examine. It appears to us to be a teratological specimen of the zoogonid *Deretrema pycnorganum* (Rees, 1953), which occurs commonly in the gall-bladder of this host off Iceland. A comparison with specimens of *D. pycnorganum* in the collections of the British Museum (Natural History) indicates that there is a great similarity in the alimentary system and the terminal genitalia. In addition, some of our specimens, especially the smaller ones, exhibit no tegumental spines, which, according to Brinkmann (1956), are also missing in *Y. anarhichae*. The 'opening of Laurer's canal', as described by Brinkmann, appears to be, in fact, the excretory pore which has been displaced onto the dorsal surface by pressure during fixation. We have no doubt, therefore, in considering *Yamagutia anarhichae* (the type-species of the genus *Prolateroporus* Yamaguti, 1971) to be a synonym of *D. pycnorganum*.

Aspects of biology

The fellodistomids have small eggs and, according to Cable (1974), miracidia with cilia confined to patches. The sporocysts develop in bivalve molluscs and the daughters normally give rise to motile cercariae. These cercariae are basically furcocercous, the excretory vesicle opening terminally on the furcae, if the latter are present. The tail, however, may be trichocercous and long, or much reduced and deciduous (see Cable, 1954). The metacercariae occur in amphipods, ctenophores and echinoderms, but in some instances the life-cycle may be telescoped, with the adults occurring in a gastropod or with the complete cycle occurring in the lamellibranch. Whilst this telescoping may occur as a general pattern in some species, other species occasionally occur as progenetic metacercariae in the second intermediate host. Apart from these examples, adult fellodistomids are found in the intestine or neighbouring organs of marine, and occasionally freshwater, teleosts. Some species exhibit a fairly rigid host-specificity, whilst others appear to be specific in part of their range and less specific in other parts. A common pattern of specificity is for the parasite to show a strong preference for a particular host species or group of species, but to occur occasionally, sometimes in an immature condition, in other hosts. The group is widespread in sub-polar, temperate and tropical waters and in both the shallows and the deeps.

Copulation is apparently reciprocal and involves the juxtaposition of the genital atria. In some species at least it involves the transfer of spermatozoa encased in fibrous spermatophores.

Key to the subfamilies of the Fellodistomidae in the northeast Atlantic

1 Caecum single (? unites with excretory vesicle) . . . . **MONASCINAE** (p. 268)
– Caeca double 2
2 Ring of conical papillae surrounding oral sucker; ridges on lateral surface of forebody; cirrus-sac bipartite; pharynx elongate . . . . **TERGESTIINAE** (p. 274)
– Body-surface lacking ornamentation; cirrus-sac oval to globular; pharynx oval . . . 3
3 Genital atrium long, narrow; seminal vesicle coiled, tubular; cirrus-sac surmounted by muscular papilla . . . . **XENOPERINAE** (p. 259)
– Genital atrium short to long; seminal vesicle bipartite 4
4 Seminal vesicle almost fills cirrus-sac; genital atrium long, narrow; vitellarium in 2, or a few, compact bunches of follicles; Laurer's canal opening at or near posterior extremity; canalicular seminal receptacle present; ovary post- or inter-testicular . . **BACCIGERINAE** (p. 248)
– Seminal vesicle small relative to size of cirrus-sac; genital atrium short, wide; vitellarium 2 (occasionally 4) lateral follicular fields; Laurer's canal opening dorsal to gonads; uterine seminal receptacle present; ovary pre-testicular . . . **FELLODISTOMINAE** (p. 202)

Subfamily FELLODISTOMINAE Nicoll, 1909

Steringophorinae Odhner, 1911.
Lissolomatinae Skrjabin & Koval, 1957.
Markevitschiellinae Skrjabin & Koval, 1957.

DIAGNOSTIC FEATURES. Body large and robust to small. Body-surface smooth. Ventral sucker usually larger than oral sucker, occasionally smaller; in middle of body or in anterior half. Pharynx globular to oval. Oesophagus absent, short or long. Caeca narrow to wide; reaching to testes or beyond and almost to posterior extremity. Testes in anterior hindbody; post-ovarian. Cirrus-sac well developed; oval to claviform; containing many prostatic gland-cells. Pars prostatica wide; straight or gently curved. Ejaculatory duct wide; pocketed. Spermatophores occasionally seen. Genital atrium small. Genital pore in mid-forebody; sinistral to median line. Ovary entire to multilobate; usually anterior to right testis. Laurer's canal and uterine seminal receptacle present. Uterus usually reaching posteriorly to testes, but does not extend into post-testicular region in type-genus. Metraterm joins genital atrium from left. Eggs numerous; operculate; small; often variable; egg-shell may be ornamented. Vitellarium follicular; in two (occasionally four) lateral fields; in fore- and/or hindbody. Excretory pore terminal; vesicle 'V'- or 'Y'-shaped; with arms reaching to level of pharynx or oral sucker. Parasitic in intestine, pyloric caeca, bile duct and gall-bladder of marine teleosts.

COMMENT. The Steringophorinae is retained as a distinct subfamily by Dollfus (1952) on the basis of the distribution of the uterus; but the present study indicates that the type-species of *Fellodistomum* Stafford, 1904, and *Steringophorus* Odhner, 1905, are similar, and that there is a form, *Steringophorus agnotus* (Nicoll, 1909), which is in some ways intermediate. We, therefore, consider it unnecessary to distinguish the Steringophorinae. The other synonyms listed, the Lissolomatinae and the Markevitschiellinae, are not well known and are not represented in our region; but it appears that *Lissoloma* Manter, 1934, is close to *Steringophorus* and *Markevitschiella* Skrjabin & Koval, 1957, is close to *Steringotrema* Odhner, 1911.

This subfamily, as represented below, is a fairly homogeneous group, and it is noticeable, for example, how similar the cirrus-sac and contents are in virtually all of the species described. The typical arrangement is well-figured and described by Nicoll (1909*a*, p. 466) and Odhner (1911*a*, p. 101). The terminology of the distal part of the male-duct is rather confusing, for as the ejaculatory duct is muscular with irregular, shallow diverticula and muscular lobations, it has been considered to be the genital atrium or sinus by some authors. These diverticula have also been termed the 'atrial diverticle' by Yamaguti (1940) in *Pseudosteringophorus* and 'atrial sac' by Manter (1947) and Armstrong (1974) in *Megalomyzon* and a number of fellodistomines, respectively. Nicoll (1909*a*), for example, states, 'at first sight the genital sinus appears to be of great size, but this is due to a wide expansion of the ductus ejaculatorius. In reality the genital sinus is comparatively small'. Our observations agree with those of Nicoll: the ejaculatory duct in relaxed specimens, we found, is always included within the cirrus-sac. The pars prostatica is a wide, straight or slightly curved vesicular structure and is lined with numerous narrow filaments which often extend into the lumen of the ejaculatory duct. These filaments appear to be involved in the formation of a fibrous spermatophore. The seminal vesicle is normally bipartite, but one or both parts may be reduced when the spermatozoa have been ejected.

The ovary in this subfamily appears in two basic forms. *Fellodistomum* and *Steringophorus* each has a distinctive acinous, multilobate ovary, while in the other genera the ovary has a smooth surface, having either a more or less globular or a trilobed shape.

A comment should be made on the unreliability of egg-measurements as taxonomic criteria in this group. As can be seen from *Steringophorus furciger* and *Steringotrema pagelli* (Tables 2 & 7) in particular, the egg-length can vary considerably, and it is apparent that in these two species at least the literature suggests that there may be an overall bimodal distribution of egg-sizes. The latter phenomenon may, however, be the result of authors measuring eggs at different stages of development.

Key to the genera of the Fellodistominae from the northeast Atlantic

1 Uterus reaching posteriorly to testes; hindbody at least as long as forebody 2
– Uterus not reaching posteriorly to testes; body almost globular; ventral sucker large . . . . *FELLODISTOMUM* Stafford, 1904 (p. 204)
2 Excretory vesicle 'Y'-shaped 3
– Excretory vesicle 'V'-shaped 4

3 Ovary multilobate; caeca reach to level of testes or, more usually, beyond; posterior limit of vitelline follicles lies posterior to anterior margin of ventral sucker; prepharynx small, indistinct . . . . ***STERINGOPHORUS*** Odhner, 1905 (p. 210)

– Ovary trilobed; caeca reach to about level of anterior margin of testes; vitelline follicles entirely in forebody; prepharynx small, distinct . . . ***OLSSONIUM*** gen. nov. (p. 228)

4 Body stout; vitellarium extending into forebody and posteriorly as far as testes, mainly in lateral fields; caeca reaching to region of testes . . ***STERINGOTREMA*** Odhner, 1911 (p. 231)

– Body elongate; vitellarium confined to hindbody, reaching well posteriorly to testes; caeca extend almost to posterior extremity . . . . . ***PRUDHOEUS*** gen. nov. (p. 245)

Genus ***FELLODISTOMUM*** Stafford, 1904

DIAGNOSTIC FEATURES. Body large; robust. Ventral sucker large; larger than oral sucker; globular; at middle of body or just posterior to it. Prepharynx short. Pharynx well developed; globular. Oesophagus absent. Caeca wide; reaching close to posterior margin of testes. Testes two; symmetrical; oval; close to posterior extremity. Cirrus-sac claviform. Seminal vesicle bipartite. Pars prostatica wide; surrounded by gland-cells. Ejaculatory duct wide; diverticulate. Genital atrium small. Genital pore close to ventral sucker; sinistrally submedian. Spermatophores may be present. Ovary multilobate; just anterior to right testis. Uterus not extending posteriorly to testes or small portion only posterior to testes [especially in flattened specimens]; bulk of uterus dorsal and lateral to ventral sucker. Eggs numerous; small; with smooth shells. Vitelline follicles in two lateral fields; lateral to and reaching just anteriorly to ventral sucker. Excretory vesicle 'Y'-shaped; stem reaching forward to anterior margin of testes; arms reaching to pharynx. Parasitic in gall-bladder of marine teleosts (Anarhichadidae).

TYPE-SPECIES. *Fellodistomum fellis* (Olsson, 1868) (by subsequent designation: Nicoll, 1909*a*: 471).

COMMENT. The present concept of the genus *Fellodistomum* includes only the large, almost globular type-species in which little or none of the uterus lies posteriorly to the testes. Our reasons for distinguishing *Steringophorus* are discussed below (p. 210). Eighteen species have, at one time or another, been assigned to this genus. These are:

(1) *F. agnotum* Nicoll, 1909, which is herein considered to be a species of *Steringophorus* (see p. 217).

(2) *F. anarhichaelupi* (Rathke, 1799) Dollfus, 1968; Dollfus (1968) used this name as a senior synonym of *F. incisum* (Rudolphi, 1809). We do not consider that either Rathke's (1799) or Rudolphi's (1809) descriptions are recognizable as species of *Fellodistomum* (see p. 209).

(3) *F. breve* Ching, 1960 (emend. Yamaguti, 1971), herein considered a species of *Steringophorus* (see p. 211).

(4) *F. fellis* (Olsson, 1868) Nicoll, 1909; type and only valid member of the genus.

(5) *F. furcigerum* (Olsson, 1868) Yamaguti, 1953; type-species of the genus *Steringophorus* (see p. 212).

(6) *F. incisum* (Rudolphi, 1809) Stafford, 1904; unrecognizable (see p. 209).

(7) *F. lethrini* (Gupta, 1956) Yamaguti, 1971; recorded from *Lethrinus* sp. from the Gulf of Manaar off India, this species was originally placed in *Steringophorus*. Yamaguti (1971), in addition to including it in *Fellodistomum* (p. 70), made it the type-species of a new genus, *Guptatrema*, which he placed in the Callodistomidae Odhner, 1910 (p. 118). Although certain marine callodistomids, e.g. *Callodistomoides* Yamaguti, 1970 (see p. 211), are difficult to distinguish from fellodistomids, *Guptatrema* appears to have characters not usually associated with the latter group, such as a long, narrow cirrus-sac, a large seminal receptacle and caeca reaching to the posterior extremity. Its position is, therefore, uncertain; but it resembles, superficially at least, *Paracryptogonimus ovatus* Yamaguti, 1952, from an unknown marine fish from off the Celebes (Yamaguti, 1952) and *Pomadasys hasta* from the Bay of Bengal (Madhavi, 1976) and *Paracryptogonimus rostratus* Nagaty & Abdel Aal, 1961, from *Lethrinus rostratus* in the Red Sea, species which are considered synonyms by Manter (1963).

(8) *F. magnum* (Manter, 1934) Yamaguti, 1953, herein considered a species of *Steringophorus* (see p. 211).

(9) *F. mendezi* Sogandares-Bernal, 1955, from the intestine of a freshwater fish, *Brachyrhaphis episcopi* in Gatun Lake, Panama. The uterus of this worm contains an average of only 10 eggs, and it is figured as possessing a considerable proportion of its uterus in the post-testicular field. As it is described mainly from a single specimen, its status is in some doubt.

(10) *F. melanostigmum* Noble & Orias, 1975, herein considered a species of the genus *Steringophorus* (see p. 211).

(11) *F. ovatum* (Price, 1934) Yamaguti, 1971; this is possibly a species of the genus *Bacciger* (see p. 249).

(12) *F. phrissovum* Aldrich, 1961, herein considered a species of the genus *Steringotrema* (see p. 232).

(13) *F. preovaricum* Caballero y C., Bravo Hollis & Grocott, 1952, from the intestine of *Galeichthys seemanni* off the Pacific coast of Panama. This species was made the type of a new genus, *Allofellodistomum*, by Yamaguti (1971). The location of the ovary in the forebody appears to justify this action, although the spinose body-surface suggests that it may not be a fellodistomid.

(14) *F. profundum* (Manter, 1934) Yamaguti, 1953, herein considered to be a species of the genus *Steringophorus* (see p. 211).

(15) *F. rotundum* (Manter, 1954) Yamaguti, 1971, herein considered to be a member of the genus *Steringotrema* (see p. 232).

(16) *F. sebastodis* Yamaguti & Matumura, 1942, herein considered to be a species of the genus *Steringophorus* (see p. 211).

(17) *F. saviniense* Dyk & Dykova, 1964, from the gall-bladder of *Salmo trutta* and *Thymallus thymallus* in the River Savinja, Yugoslavia. It seems likely that this species belongs to the zoogonid genus *Pseudochetosoma* Dollfus, 1951, which contains species from the gall-bladder of freshwater fishes in central Europe (Kakacheva-Avramova, 1966*a*, 1966*b*).

(18) *F. thapari* Srivastava & Ghosh, 1968; a synonym of *F. fellis.*

Fellodistomum fellis (Olsson, 1868) Nicoll, 1909

Distoma fellis Olsson, 1868.
Distoma incisum Rudolphi of van Beneden (1871).
Fellodistomum incisum (Rudolphi) of Stafford (1904) in part (?).
(?) *Cercaria limae* Nicoll & Small, 1909.
(?) *Metacercaria limae* (Nicoll & Small) James, Sannia & Bowers, 1977.
Adolescaria ophiurae Tauson, 1917.
Fellodistomum thapari Srivastava & Ghosh, 1968.

TYPE-HOST AND LOCALITY. *Anarhichas lupus*, Varberg, Sweden.

RECORDS

(i) Material studied

(a) From the NE Atlantic

Anarhichas lupus [gall-bladder] Iceland (see Rees, 1953: 15). BM(NH) 1976.4.8.179.
—— [gall-bladder] Herdla, Norway (July, 1971). Material of J. Thulin.
—— [gall-bladder] Eldey Bank, off Reykjanes, Iceland (64°N, 24°W; depth 148–152 m; May, 1974). BM(NH) 1977.3.1.1–20.
—— [gall-bladder] Orkney Islands, Scotland (59°N, 04°W; depth 164–172 m; July, 1976). BM(NH) 1977.3.1.21–40.
—— [gall-bladder] Moray Firth, Scotland (58°N, 02°W; depth 164 m; July, 1976). BM(NH) 1977.3.1.21–40.

(b) From elsewhere

Anarhichas denticulatus [gall-bladder] Newfoundland (see Bray, 1979 : 419). BM(NH) 1977.2.15.202–203.

Anarhichas lupus [gall-bladder] Locality unknown; donated by Zoological Museum, Amsterdam. BM(NH) 1946.12.20.1–20.
—— [gall-bladder] Newfoundland (see Bray, 1979 : 419). BM(NH) 1977.2.15.186–200.
Anarhichas minor [gall-bladder] Newfoundland (see Bray, 1979 : 419). BM(NH) 1977.2.15.201.

(ii) NE Atlantic records from the literature
Anarhichas lupus [gall-bladder & intestine] Varberg, Sweden (July, Aug.). Olsson (1868 : 44; as *Distoma fellis*).
—— [gall-bladder & intestine] Belgian coast. van Beneden (1871 : 48; as *Distoma incisum*);
—— [gall-bladder] North Sea (Feb., 1893). Jacoby (1899 : 12; as *Distomum fellis*).
—— [gall-bladder] Northumberland, England. Lebour (1908*a* : 36; as *Distomum fellis*).
—— [gall-bladder] St Andrews, Fife, Scotland. Nicoll (1909*a* : 458).
—— [gall-bladder] East coast of Iceland (66°N, 13°W; depth 119 m; Aug. 1948). Rees (1953 : 15).
—— [gall-bladder] Reykjavik, Neskaupstadur & Húsavík, Iceland (June, July 1955). Brinkmann (1956 : 20).
Anarhichas minor [gall-bladder] Neskaupstadur & Húsavík, Iceland (July, 1955). Brinkmann (1956 : 20).
—— [gall-bladder] Umîvik, East Greenland (July, 1959). Brinkmann (1975 : 51).

ASPECTS OF BIOLOGY. Records of intermediate hosts in the NE Atlantic:
(a) First intermediate host
Nil.
(b) Second intermediate host
Ophiura albida [stomach] Kristineberg, Sweden. Mortensen (1920 : 67; identification by T. Odhner).
[?] *Lima hians* [mantle] Millport, Firth of Clyde, Scotland. Nicoll & Small (1909 : 241; as *Cercaria limae*).
[?] *Macoma baltica* [?] Burry Inlet, South Wales. James, Sannia & Bowers (1977 : 13; as *Metacercaria limae*).

The life-history of this species has been studied by Chubrik (1952, 1966) in the Barents Sea. This author states that the sporocysts develop in the bivalve *Nucula tenuis* and the daughters contain 7–10 cercariae. These cercariae are non-oculate, brevifurcate and distomatous, possessing an almost 'V'-shaped excretory vesicle with its base forming a reservoir. The tail is broad and flat. The metacercariae are found in the digestive tract of echinoderms of the genus *Ophiura* and progenesis occasionally occurs. *Adolescaria ophiurae*, described by Tauson (1917) from *Ophiura sarsi* in the Barents Sea, is so similar to the *Fellodistomum* metacercariae described by Chubrik that there can be little doubt of its identity with *F. fellis*. A similar worm, *Cercaria limae*, was described from the gaping file-shell bivalve, *Lima hians*, by Nicoll & Small (1909). Single encysted specimens were found loosely attached to the underside of the mantle-edge, projecting into the mantle-cavity of two file-shells. Nicoll & Small considered that the evidence strongly suggested that they were *F. fellis;* but that they could also belong to a species of *Steringophorus*, particularly as *Anarchichas lupus* was rare in their area. This same worm has also been found recently by James *et al.* (1977) in the Baltic tellin *Macoma baltica* from south Wales.

This species normally occurs in the gall-bladder of anarhichadid fishes, sometimes in great numbers (over 4000, according to Polyanski, 1955); but it is occasionally found in the intestine or urinary bladder (Olsson, 1868; van Beneden, 1871; Polyanski, 1955). In addition, Polyanski (1955) found immature specimens in the intestine and gall-bladder of the plaice *Pleuronectes platessa*, and Srivastava & Ghosh (1968) record their *Fellodistomum thapari* from the gall-bladder of the anglerfish *Lophius piscatorius* and from the intestine of *Anarhichas lupus*. A study of the literature indicates that *F. fellis* is restricted to the northern Atlantic Ocean and the Barents Sea.

We found two specimens which are apparently in the act of copulation (Fig. 1d). The genital pores are juxtaposed with the forebodies of each worm at an acute angle to each other. When separated, structures interpreted as being spermatophores were seen, apparently having been expelled from the genital pore of both worms, lying close to these pores. In sections, the fibrous coat of the spermatophore can be traced back to the cells lining the pars prostatica (Fig. 2). The bipartite seminal vesicle in one of this pair which was sectioned contained very few spermatozoa. It seems likely, therefore, that sperm-transfer takes place via the metraterm and not via Laurer's canal.

Previous descriptions. Olsson (1868 : 44; as *Distoma fellis*); Jacoby (1899 : 12; as *Distomum fellis*); Nicoll (1909*a* : 458); Miller (1941 : 43); Rees (1953 : 15); Polyanski (1955 : 20); Srivastava & Ghosh (1968 : 46; as *F. thapari*).

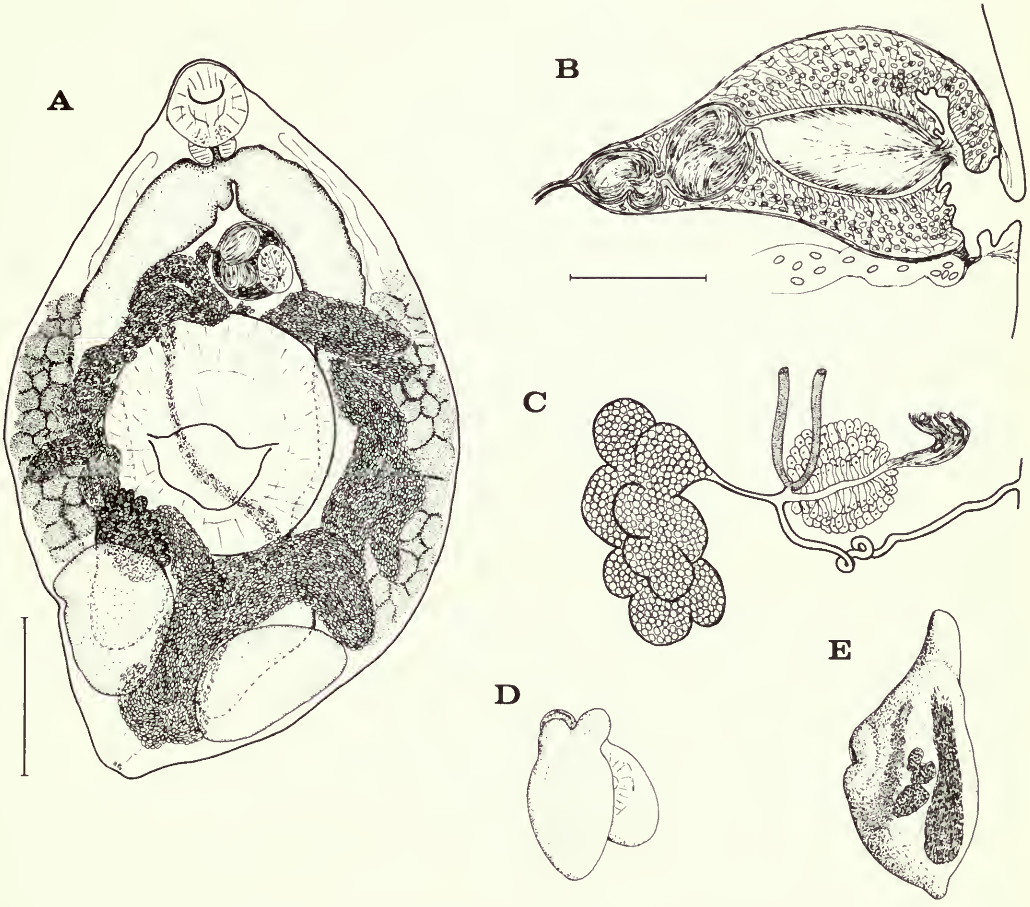


Fig. 1 *Fellodistomum fellis:* (a) slightly flattened whole mount; (b) cirrus-sac; (c) diagram of female proximal genitalia; (d) two worms in copulation (free-hand sketch); (e) lateral view of fixed but unflattened worm (free-hand sketch). Bar scales: a = 1 mm; b = 0·25 mm.

Description (Figs 1 & 2). This description is based upon 38 whole-mounted and three serially sectioned specimens which represent a wide range of sizes and states of maturity. The dimensions of these worms, in addition to some measurements from the literature, are included in Table 1.

The adult worms are stout (Fig. 1e) and are almost subglobular with an anterior protuberance carrying the oral sucker in addition to a small posterior protuberance. The body-wall is thin and unarmed. The subglobular *oral sucker* opens subterminally, and the large, globular *ventral sucker* is deeply embedded in the middle of the body (Fig. 1a). The ventral sucker is invariably much broader than the oral sucker, in the ratio of 1 : 1·5–3·0, with a distinct tendency for the ratio in

Table 1 Dimensions of *Fellodistomum fellis* from the present material and from the literature

Authority	Jacoby (1899)	Nicoll (1909*a*)	Rees (1953)	Present material
Name used	*Distomum fellis*	*Fellodistomum fellis*	*Fellodistomum fellis*	*Fellodistomum fellis*
Hosts	*Anarhichas lupus*	*Anarhichas lupus*	*Anarhichas lupus*	see text
Locality	North Sea	Scotland	Iceland	see text
Length (mm)	2–2·5	2·5–3·3	2·5–3·3*	0·97–3·7*
Breadth (mm)	1	1·1–1·6	1·1–1·8	0·38–2·44
Length : forebody ratio	(1 : 0·41)	–	–	1 : 0·23–0·48
Oral sucker (mm)	0·36 dia.	0·40–0·45 dia.	0·40–0·45	0·18–0·56 × 0·22–0·67
Ventral sucker (mm)	0·88 dia.	0·9–1·0 dia.	0·90–1·50	0·34–1·62 × 0·33–1·84
Sucker-ratio	(1 : 1·9)	–	1 : 2·25–3	1 : 1·5–3·0
Pharynx (mm)	0·22 dia.	0·16–0·21 long	0·18–0·21	0·13–0·27 × 0·13–0·28
Cirrus-sac (mm)	0·29 × 0·23	–	–	0·92 × 0·39†
Testes (mm)	–	0·45 × 0·19	–	0·10–0·80 × 0·09–0·60
Ovary (mm)	–	–	–	0·42 × 0·22†
Eggs (μm)	40 × 20	42 × 23	42–43 × 23–24	37–48 × 19–29

* Some measurements from flattened specimens.
† Measured from sections.

the larger worms to be greater than in the smaller. The oral sucker is connected by a short prepharynx (visible only in sections) to a globular *pharynx*. There is no oesophagus as the intestine divides immediately on leaving the pharynx and forms two wide, but thin-walled, caeca, which are almost invariably filled with the semi-digested remains of blood-cells. This opaque mass often obscures much of the internal details of the worm in whole-mounts. The caeca, which are apparently lined with squamous epithelium, run in the dorso-lateral fields and terminate blindly at the level of the testes.

The *excretory pore* lies terminally and leads via a short, narrow duct into the wide stem of the excretory vesicle, which reaches to the anterior margin of the testes. At this point narrow arms arise which pass dorso-laterally to the ventral sucker and expand slightly in the forebody. They terminate laterally at the level of the pharynx.

The irregular but more or less oval *testes* lie symmetrically close to the posterior extremity. The two vasa efferentia unite to form the seminal vesicle immediately after passing through the base of the thin-walled *cirrus-sac*. The latter structure lies just anteriorly to the ventral sucker. As it lies more or less perpendicularly to the ventral surface, the measurement for it given in Table 1 is taken from longitudinal sections. It is claviform in shape, narrowing proximally, and contains, in addition to a bipartite seminal vesicle, a wide pars prostatica and a wide, irregular ejaculatory duct (Fig. 1b). The proximal part of the seminal vesicle may be slightly coiled, and occasionally one or both parts may be reduced to a narrow duct, especially when a spermatophore is present. The wider distal part of the cirrus-sac contains the dilate pars prostatica which is surrounded by a dense mass of gland-cells and lined by numerous filamentous projections. These projections extend forward into the ejaculatory duct through a narrow opening and appear to be involved in the formation of the wall of the spermatophore (Fig. 2). The ejaculatory duct is large and may be mistaken for a genital atrium. Its wall is strongly muscular and forms numerous irregular pockets and lobes. The genital atrium itself is small and opens, via the genital pore, in the posterior region of the forebody just to the left of the median line.

The multilobate *ovary* lies close to the anterior margin of the right testis. From it a narrow oviduct passes dorsally, leading to a diffuse Mehlis' gland. Laurer's canal, which opens dorsally at about the level of the ovary, and a minute common vitelline duct open into the oviduct just prior to its entry into Mehlis' gland (Fig. 1c). The initial coils of the *uterus* form a uterine seminal receptacle, there being no other seminal storage organ in the female part of the reproductive

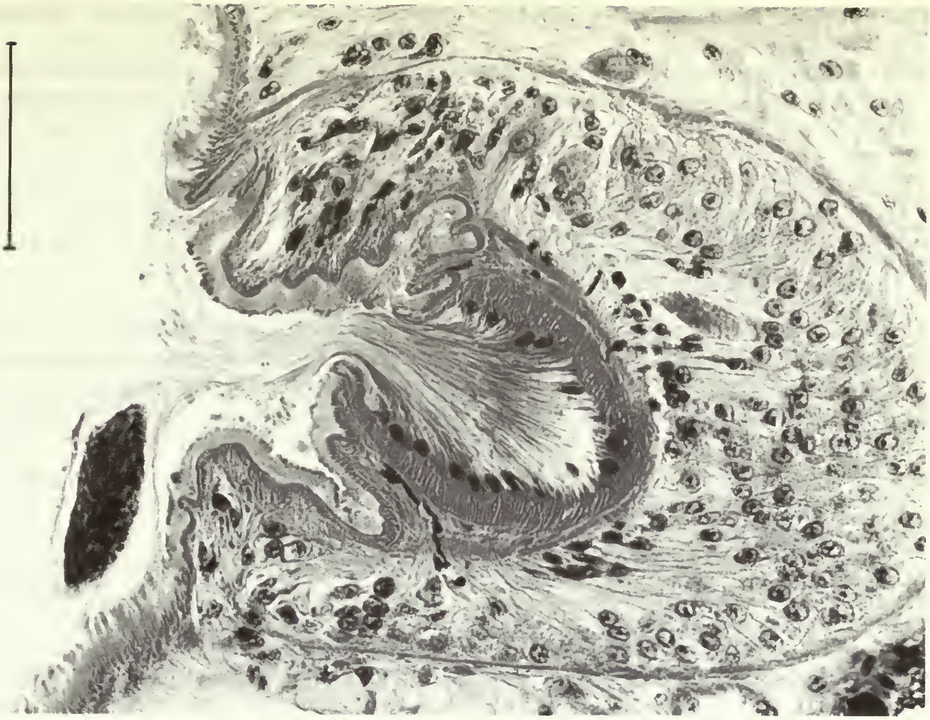


Fig. 2 Photomicrograph of section showing spermatophore production in *Fellodistomum fellis*. Bar scale: =0·1 mm.

system. The uterine coils extend posteriorly between, or fractionally beyond, the testes; but the great bulk of the uterus occurs between the testes and the cirrus-sac, especially around the ventral sucker. The distal extremity of the uterus, which is thin-walled and wide, enters the genital atrium posteriorly through a muscular sphincter (Fig. 1b). The numerous eggs which fill the uterus are operculate and possess a smooth shell. The vitellarium consists of a number of irregular follicles of varying sizes, which are packed tightly in lateral fields between the anterior margins of the testes and the anterior margin of the ventral sucker or the cirrus-sac. There are two main lateral vitelline ducts at the level of the ovary which pass medially and unite to form the short common vitelline duct immediately prior to uniting with the oviduct.

Discussion. *Distomum fellis* of Olsson (1868) is the earliest name that can unequivocally be used for this species. Older names, such as *Distoma anarhichaelupi* Rathke, 1799, and *D. incisum* Rudolphi, 1809, from the stomach of *Anarhichas lupus*, cannot be compared as the descriptions are totally inadequate. In addition, these names have fallen out of use since Nicoll (1909*a*), who discussed their validity at some length, came to the same conclusion. The figure of *Distoma incisum* produced by van Beneden (1871) strongly suggests that he was dealing with *F. fellis:* we have, therefore, included this as a synonym. The genus *Fellodistomum* was initially erected by Stafford (1904) based on his very brief description of '*F. incisum*'; but his specimens were redescribed by Miller (1941), who came to the conclusion that they were *F. fellis*.

Srivastava & Ghosh (1968) described a new species, *F. thapari*, from the gall-bladder of *Lophius piscatorius* and the intestine of *Anarhichas lupus* from an unknown locality [neither of these two fishes occur outside the North Atlantic region or, in the case of *A. lupus*, the Arctic Ocean; the material came from the collection of the late Dr G. S. Thapar]. There appears to be no reason to consider this species distinct from *F. fellis*. Three of the four differentiating features mentioned by these authors were probably produced by the flattening which appears to have been carried out on their specimens. The other feature, the sucker-ratio, lies in the middle of the range of the present material.

Fellodistomum agnotum Nicoll, 1909, was considered by Dawes (1947) to be a further synonym of *F. fellis*; but in this work we consider this form to be a species of *Steringophorus* (see p. 219).

Genus ***STERINGOPHORUS*** Odhner, 1905

Leioderma Stafford, 1904, *nec* Willemoes-Suhm, 1873.
Callodistomoides Yamaguti, 1970.
Abyssotrema Campbell, 1975.

Diagnostic features. Body large; deep-bodied to dorso-ventrally flattened. Ventral sucker usually larger than oral sucker; in anterior half of body. Prepharynx short or apparently absent. Pharynx well developed; globular. Oesophagus absent to long. Caecal bifurcation anterior to or at level of genital pore; caeca wide to narrow; reaching to testes, to about middle of post-testicular region or occasionally beyond. Testes oval, indented or deeply lobed; symmetrical to tandem. Cirrus-sac oval. Seminal vesicle bipartite. Pars prostatica wide; surrounded by gland-cells. Ejaculatory duct wide; diverticulate. Genital atrium small. Spermatophores may be present. Genital pore close to anterior margin of ventral sucker; sinistral to median line. Ovary multilobed; just pre-testicular. Uterus mainly coiled posteriorly to testes. Eggs numerous; small; shells occasionally ornamented. Vitelline follicles in two lateral fields between level of caecal bifurcation and level just posterior to testes. Excretory vesicle 'Y'-shaped; stem reaching to between middle of post-testicular region and about level of testes; arms extending into forebody. Parasitic in intestine (occasionally body-cavity, gall-bladder, bile-ducts, etc.) of marine teleosts.

Type-Species. *Steringophorus furciger* (Olsson, 1868) (by original designation).

Comment. Yamaguti (1971) considers that *Fellodistomum* is an immature form of *Steringophorus* on the basis that the distribution of the uterus in the former genus does not extend into the post-testicular region. He presents this argument to support his belief that *Steringophorus* is a synonym of *Fellodistomum* which he first propounded in 1953. Our studies have shown, however, that even in immature specimens of *Steringophorus*, the primordium of the uterus extends into the post-testicular field. This condition is illustrated by Polyanski (1955, fig. 21B) in *Steringophorus furciger*, and we have seen it both in that species and in *S. agnotus* (Nicoll, 1909), the species of this genus which is considered to be most similar to *Fellodistomum*. In fact this difference between the genera is even more distinct because the pre-testicular part of the uterus in *Steringophorus* only fills with eggs to any significant extent in the older and larger specimens. In *Steringophorus* the post-testicular part of the uterus takes up a variety of forms, being, for example, a single convoluted loop in *S. agnotus*, a pair of lateral convoluted loops in *S. blackeri* Bray, 1973, and a complex arrangement filling much of the hindbody in *S. furciger*.

We have included the genus *Abyssotrema* Campbell, 1975, as a synonym of *Steringophorus*. Campbell (1975) placed this genus in the subfamily Monascinae, which he distinguished from the Fellodistominae by the position of the cirrus-sac ('preacetabular' in the Fellodistominae), the configuration of the testes ('symmetrical' in the Fellodistominae) and the position of the vitellarium ('preacetabular or rarely in acetabulotesticular zone' in the Fellodistominae). As can be seen from the present work, only the statement concerning the testicular configuration appears to be valid. Campbell also states that the fellodistomines (along with the Heterorchiinae) typically possess an ovary with a smooth margin, but again the present work shows that this is not the case. In fact *Abyssotrema* is similar to the known species of *Steringophorus*, differing significantly only in the configuration of the testes, which on its own does not seem to be a character of generic importance.

Campbell (1975) also compared *Abyssotrema* with the members of the Heterorchiinae, i.e. *Heterorchis* Baylis, 1915; *Mesolecitha* Linton, 1910; and *Elopsium* Fischthal & Thomas, 1972. *Heterorchis*, which occurs in lung-fishes and anurans in Africa, differs considerably from *Abyssotrema*, and from other fellodistomids, in many features and is probably best considered as a member of the Plagiorchiidae Lühe, 1901 (see Prudhoe & Bray, in press). *Mesolecitha* differs from *Abyssotrema*, and other fellodistomids, in possessing a spiny body-surface, a more elongate cirrus-sac, a dextral genital pore and a sinistral ovary (Linton, 1910; Fischthal & Thomas, 1968), although Manter (1947) could not confirm that spines were present on the body-surface and found the genital pore to be sinistral: he also found spines on the cirrus and metraterm. *Mesolecitha* also differs from *Abyssotrema* in having an entire ovary and a tendency for the vitelline fields to fuse medially. Campbell considered the genus most similar to *Abyssotrema* to be *Elopsium* Fischthal & Thomas, 1972 (syn. *Protomonascus* Thulin, 1973; see Thulin, 1974). It differs in the shape of the cirrus-sac, the coiled, tubular nature of the seminal vesicle, the narrow pars prostatica, the smaller ejaculatory duct, the longer caeca, the more posterior and more oblique position of the testes, the gonads widely separated by coils of the uterus and the more extensive vitellarium. The systematic position of *Elopsium* is not straightforward, but it does appear to be a fellodistomid.

Of the 14 species which have been assigned to the genus *Steringophorus* 11 are herein considered valid. They are:

(1) *Steringophorus agnotus* (Nicoll, 1909) Dollfus, 1952 (see p. 217).
(2) *S. brevis* (Ching, 1960) n. comb; described as *Fellodistomum brevis* from a single specimen taken from the intestine of the pleuronectid fish *Microstomus pacificus* at Friday Harbour, Washington State, USA. It possesses post-testicular uterine coils, a short oesophagus and other characters which indicate that it is a species of *Steringophorus*.
(3) *S. blackeri* Bray, 1973 (see p. 220).
(4) *S. foliatus* (Yamaguti, 1970) n. comb.; described as *Callodistomoides foliatus* from the intestine of *Emmelichthyops* sp. off Hawaii. It possesses lobed testes and is, therefore, similar to *S. thulini* sp. nov., but the caeca reach almost to the posterior extremity. Yamaguti (1970) described 'well-sclerotized gonotyles' which are apparently the irregularities in the wall of the ejaculatory duct which are seen in many fellodistomines. The cirrus-sac, therefore, exhibits a typical *Steringophorus* arrangement (see Yamaguti, 1970, Fig. 53B).
(5) *S. furciger* (Olsson, 1868) Odhner, 1905; type-species of the genus (see p. 212).
(6) *S. magnus* Manter, 1934; described from the intestine of an unidentified eel-like fish off Florida.
(7) *S. melanostigma* (Noble & Orias, 1975) n. comb., described as *Fellodistomum melanostigmum* from the intestine of *Melanostigma pammelas* off southern California. It is similar to *S. furciger* and to three of the other species from deeper waters, i.e. *S. blackeri*, *S. magnus* and *S. profundum* Manter, 1934. We have emended the suffix on the specific name.
(8) *S. pritchardae* (Campbell, 1975) n. comb. (see p. 223).
(9) *S. profundum* Manter, 1934; described from the intestine of *Argentina striata* off Florida.
(10) *S. sebastodis* (Yamaguti & Matumura, 1942) Dollfus, 1952; described as *Fellodistomum sebastodis* from the gall-bladder of *Sebastodes* spp. in the northern Pacific Ocean. This species has a number of characteristics in common with *S. agnotus*.
(11) *S. thulini* sp. nov. (see p. 226).

The three species not considered to belong to *Steringophorus* are:

(1) *S. cluthense* Nicoll, 1909; the type-species of the genus *Steringotrema* and a synonym of *Steringotrema pagelli* (see p. 234).
(2) *S. lethrini* Gupta, 1956; a species of doubtful status (see *Fellodistomum lethrini*, p. 204).
(3) *S. ovacutus* Lebour, 1908; herein considered a species of *Steringotrema* (see p. 242).

Key to the species of *Steringophorus* recorded from the northeast Atlantic

– Vitellarium partly in forebody; caeca reach back to level of testes or only just beyond; post-testicular region of uterus a single convoluted loop (occasionally a few loops) . . . . **S. agnotus** (Nicoll, 1909) (p. 217)
– Vitellarium not reaching into forebody; caeca reaching beyond testes up to half-way along post-testicular field; post-testicular region of uterus composed of two to many convoluted loops . 2

2 Testes tandem; bifurcation of excretory vesicle in middle of post-testicular region . . . . **S. pritchardae** (Campbell, 1975) (p. 223)

– Testes symmetrical to oblique; bifurcation of excretory vesicle further forward than middle of post-testicular region 3

3 Vitellarium not reaching posteriorly to testes, with closely packed irregular follicles; uterus irregularly coiled across centre of hindbody; eggs with smooth shells 4

– Vitellarium reaching just posteriorly to testes, follicles short and tubular to globular; uterus coiled in two (occasionally one) lateral, convoluted loops in post-testicular region, with significant part of hindbody lacking coils of the uterus; egg-shells ornamented with tubercles . . . . **S. blackeri** Bray, 1973 (p. 220)

4 Testes with smooth or slightly indented margins; sucker-ratio 1 : 1·5–2·3; eggs 42–54 (usually 46–52) (possibly up to 68) µm long; large ejaculatory duct, small seminal vesicle . . . . **S. furciger** (Olsson, 1868) (p. 212)

– Testes deeply lobed; sucker-ratio 1 : 1·2–1·75; eggs 36–43 (usually 38–42) µm long; small ejaculatory duct, large seminal vesicle . . . . . . **S. thulini** sp. nov. (p. 226)

Steringophorus furciger (Olsson, 1868) Odhner, 1905

Distoma furcigerum Olsson, 1868.
Distoma (*Dicrocoelium*) *furcigerum* (Olsson) Stossich, 1886.
Leioderma furcigerum (Olsson) Stafford, 1904.
Fellodistomum furcigerum (Olsson) Yamaguti, 1953.

TYPE-HOST AND LOCALITY. *Limanda limanda*, Varberg, Sweden.

RECORDS

(i) Material studied

(a) From the NE Atlantic

Anarhichas denticulatus [intestine] Iceland–Faroes channel (64°N, 10°W; depth 592–620 m; June, 1974). BM(NH) 1977.3.2.3–8.

Glyptocephalus cynoglossus [intestine] Gothenburg, Sweden (Sept. 1973). Material of J. Thulin.

—— [intestine] Moray Firth, Scotland (58°N, 02°W; depth 89–140 m; July, 1976). BM(NH) 1977.3.2.1.

Hippoglossoides platessoides [intestine] Aberdeen, Scotland (Oct., 73). BM(NH) 1978.1.30.1–4.

—— [intestine] Shetland Isles, Scotland (60°N, 01°E; depth 136–144 m; July, 1976). BM(NH) 1977.3.2.2.

Limanda limanda [intestine] Cullercoats, Northumberland, England (May, 1972). Material of J. Thulin.

Lycenchelys sarsi [intestine] Tjärnö, Sweden (June, 1971). Material of J. Thulin.

Lycodes esmarki [intestine] Foula, off NW Scotland (60°N, 06°W; depth 1000–1020 m; June, 1974). BM(NH) 1977. 3.2.9–12.

Lycodes vahli [intestine] Mid-Skagerrak, between Denmark and Sweden (Dec., 1970). Material of J. Thulin.

—— [intestine] Tjärnö, Sweden (June, 1971) Material of J Thulin.

Lycodes sp. [intestine] Iceland–Faroes channel (64°N, 10°W; depth 720–748 m; June, 1974). BM(NH) 1977.3.2.13–15.

Microstomus kitt [intestine] Tjärnö, Sweden (June, 1971). Material of J. Thulin.

Reinhardtius hippoglossoides [intestine] NNE of Rona, Scotland (60°N, 05°W; depth 770–800 m; April, 1973). BM(NH) 1977.3.2.16.

—— [intestine] Anton Dohrn Bank, East Greenland (66°N, 30°W; depth 380–390 m; May, 1973). BM(NH) 1977.3.2.17.

—— [intestine] Iceland–Faroes channel (63°N, 11°W; depth 410–420 m; June, 1974). BM(NH) 1977.3.2.18.

(b) From elsewhere

Anarhichas minor [intestine] Newfoundland (see Bray, 1979 : 419). BM(NH) 1977.2.16.1.

Glyptocephalus cynoglossus [intestine] Newfoundland, Labrador and Nova Scotia (see Bray, 1979 : 419). BM(NH) 1977.2.16.2–12.

Hippoglossoides platessoides [intestine] Newfoundland (see Bray, 1979 : 420). BM(NH) 1977.2.16. 13–50.

Limanda ferruginea [intestine] Nova Scotia (see Bray, 1979 : 420). BM(NH) 1977.2.16.51–52.

Myoxocephalus octodecemspinosus [intestine] Nova Scotia (see Bray, 1979 : 420). BM(NH) 1977.2.16.53.

Urophycis tenuis [intestine] Newfoundland (see Bray, 1979 : 420). BM(NH) 1977.2.16.54.

(ii) NE Atlantic records from the literature

[?] *Gadus morhua* [pylorus] Locality not given. McLaren & Hockley (1977 : 147) [this would appear to be a questionable record].

Glyptocephalus cynoglossus [intestine] Northumberland, England. Lebour (1908*a* : 33).

—— [intestine] Aberdeen, Scotland. Nicoll (1913 : 190).

Gymnacanthus tricuspis [intestine] East Greenland. Odhner (1905 : 305).

Hippoglossoides platessoides [stomach & intestine] Varberg (Aug.) and Øresund (May), Sweden. Olsson (1868 : 26; as *Distoma furcigerum*).

—— [intestine] Northumberland, England. Lebour (1908*a* : 33).

—— [intestine] Aberdeen, Scotland. Nicoll (1913 : 190).

—— [intestine] Øresund. Køie (1979: 127).

Limanda limanda [stomach & intestine] Varberg, Sweden (July, Aug.). Olsson (1868 : 26; as *Distoma furcigerum*).

—— [intestine] West coast of Sweden. Odhner (1905 : 305).

—— [stomach & intestine] St Andrews, Fife, Scotland. Nicoll (1907 : 72).

—— [intestine] Northumberland, England. Lebour (1908*a* : 33).

—— [intestine] Millport, Firth of Clyde, Scotland. Nicoll (1910 : 347; as *Leioderma furcigerum*).

—— [intestine] Aberdeen, Scotland. Nicoll (1915*a* : 360).

—— [intestine] Galway, Ireland. Little (1929 : 26, 27).

—— [intestine] Øresund. Køie (1979: 127).

Lophius piscatorius [intestine] Northumberland, England. Lebour (1908*a* : 33 – probably a 'fortuitous' host – Nicoll, 1909*b* : 16).

Lycodes pallidus [intestine] East Greenland. Odhner (1905 : 305).

Microstomus kitt [intestine] Northumberland, England. Lebour (1908*a* : 33).

Pleuronectes platessa [intestine] Northumberland, England. Lebour (1908*a* : 33).

—— [intestine] Øresund. Køie (1979: 127).

ASPECTS OF BIOLOGY. Records of intermediate hosts in the NE Atlantic.

(a) Intermediate hosts

Nuculana minuta [?] Øresund. Køie (1979: 124).

(b) (?) Accidental invertebrate host.

Buccinum undatum [stomach & oesophageal caecum] Øresund. Køie (1969 : 266).

Neptunea antiqua [?] Øresund. Køie (1979: 126).

Chubrik (1966) stated that the sporocysts and cercariae occur in the bivalve *Nuculana pernula* in the Barents Sea region and Køie (1979) found *N. minuta* infested in Øresund and west Greenland. The large, cylindrical daughter-sporocysts contain 30–70 developing cercariae, which differ from those reckoned to be *Fellodistomum fellis* in that they lack furcae on the long, narrow tail and have a distinctly 'Y'-shaped excretory vesicle. Køie (1969) and Yamaguti (1975) point out that the metacercaria is not known, although the encysted worms found by Nicoll & Small (1909) (see p. 206) may belong to this genus. Køie (1969) has repeatedly found immature *S. furciger* in the common whelk *Buccinum undatum* in Øresund between Denmark and Sweden, but never at Kristineberg or Gullmarfjord to the north. Although the same size as those from fish, they were rarely found with fully-developed eggs. Køie considered that the whelk is an accidental host. She points out that the whelk has roughly the same diet as the flatfishes which are the most common hosts of this parasite. Scott (1975*a*) found no clues as to the identity of the second intermediate host when he discovered that there was no obvious relationships between incidence and fish-length in infestations of *Hippoglossoides platessoides* in the north-west Atlantic.

Recently, Køie (1979) has shown that, in fact, the metacercarial stage is omitted, the final host feeding directly on the cercaria.

Levinsen's (1881) description and our own observations indicate that spermatophores may be formed by this worm.

Although flatfishes appear to be the most frequent hosts of this parasite, it also occurs in a variety of other fishes, especially eelpouts. It has a circumpolar distribution, having been found across northernmost regions of the Atlantic and Pacific Oceans, as well as in the Barents, White and Kara Seas. Although reaching as far south as Massachusetts in the western North Atlantic (Linton, 1940) and Britain and Ireland in the east, its main area of distribution is probably in the sub-arctic and arctic seas. In the Pacific its known southern limits are Japan in the west (Yamaguti, 1934) and Washington State in the east (Ching, 1960). We have examined the specimens recorded from the English Channel at Plymouth by Baylis & Jones (1933) and Baylis (1939), and we consider them to be immature specimens of *Steringotrema pagelli* (van Beneden, 1871).

In the waters off the eastern coast of Canada this parasite may be a biological indicator ('tag') for stocks of the long rough dab *Hippoglossoides platessoides*. Scott (1975*b*) found a high incidence in the Gulf of St Lawrence and a lower incidence in other Canadian fishing grounds, and he pointed out that this supports other evidence that the Gulf of St Lawrence stock is distinct.

PREVIOUS DESCRIPTIONS. Olsson (1868 : 28; as *Distoma furcigerum*); Levinsen (1881 : 61; as *Distomum furcigerum*); Odhner (1905 : 305); Lebour (1908*a* : 33); Yamaguti (1934 : 405); Linton (1940 : 39); Miller (1941 : 44); Polyansky (1955 : 52); Strelkov (1960 : 156).

DESCRIPTION (Fig. 3). This description is based upon 92 whole-mounted and 6 serially sectioned specimens. These worms have an elongate oval body-shape, being more or less fusiform in young specimens (Fig. 3b) and possessing an elongate, parallel-sided hindbody in older worms (Fig. 3a). The body-surface is smooth. The dimensions of the worms are summarized in Table 2.

The subterminal, globular *oral sucker* is smaller than the slightly transversely elongate-oval *ventral sucker*, the ratio being 1 : 1·5–2·3. In young specimens the ventral sucker is situated at about one-third of the body-length from the anterior end, but in older specimens it becomes more anteriorly situated as the hindbody grows allometrically. The parenchymal cells of the body of this worm envelop numerous patches of glandular cells, which also occur embedded less densely in the musculature of the suckers. There is a small prepharynx which leads into a subglobular *pharynx*, and this in turn leads into an oesophagus that is usually about the same length or a little longer than the pharynx. The intestinal bifurcation occurs at the level of the genital pore, and two narrow caeca pass back beyond the testes, but terminate prior to reaching the middle of the post-testicular zone.

The terminal *excretory pore* leads into a 'Y'-shaped vesicle, the stem of which reaches forward to the testes before bifurcating. The arms of the vesicle pass between the testes, then dorso-laterally to the ventral sucker and into the forebody as far as the pharynx.

The *testes* lie in the anterior half of the hindbody in a more or less symmetrical arrangement. Their margins are smooth or slightly indented. The narrow vasa efferentia enter the cirrus-sac separately, but close together. The *cirrus-sac* is a large, oval structure lying just anteriorly to the ventral sucker and overlapping it to a small extent. It contains a bipartite seminal vesicle of variable size, the proximal part of which is often smaller and contains less sperm than the distal part (Fig. 3d), but both parts may be empty and therefore narrow (Fig. 3c). The wide pars prostatica is similar to that of *Fellodistomum fellis* in shape and in the nature of the lining and the wide, irregular ejaculatory duct is also similar. The genital atrium is quite small compared with the ejaculatory duct and opens, via the genital pore, just posterior to the middle of the forebody to the left of the median line.

Immediately antero-dextral to the right testis lies the multilobate *ovary*. The oviduct arises posteriorly and receives Laurer's canal and a narrow common vitelline duct before entering a large Mehlis' gland, which lies directly posterior to the ovary. Laurer's canal is short and opens dorsally at the level of the posterior margin of the ovary. The *uterus* passes anteriorly from Mehlis' gland,

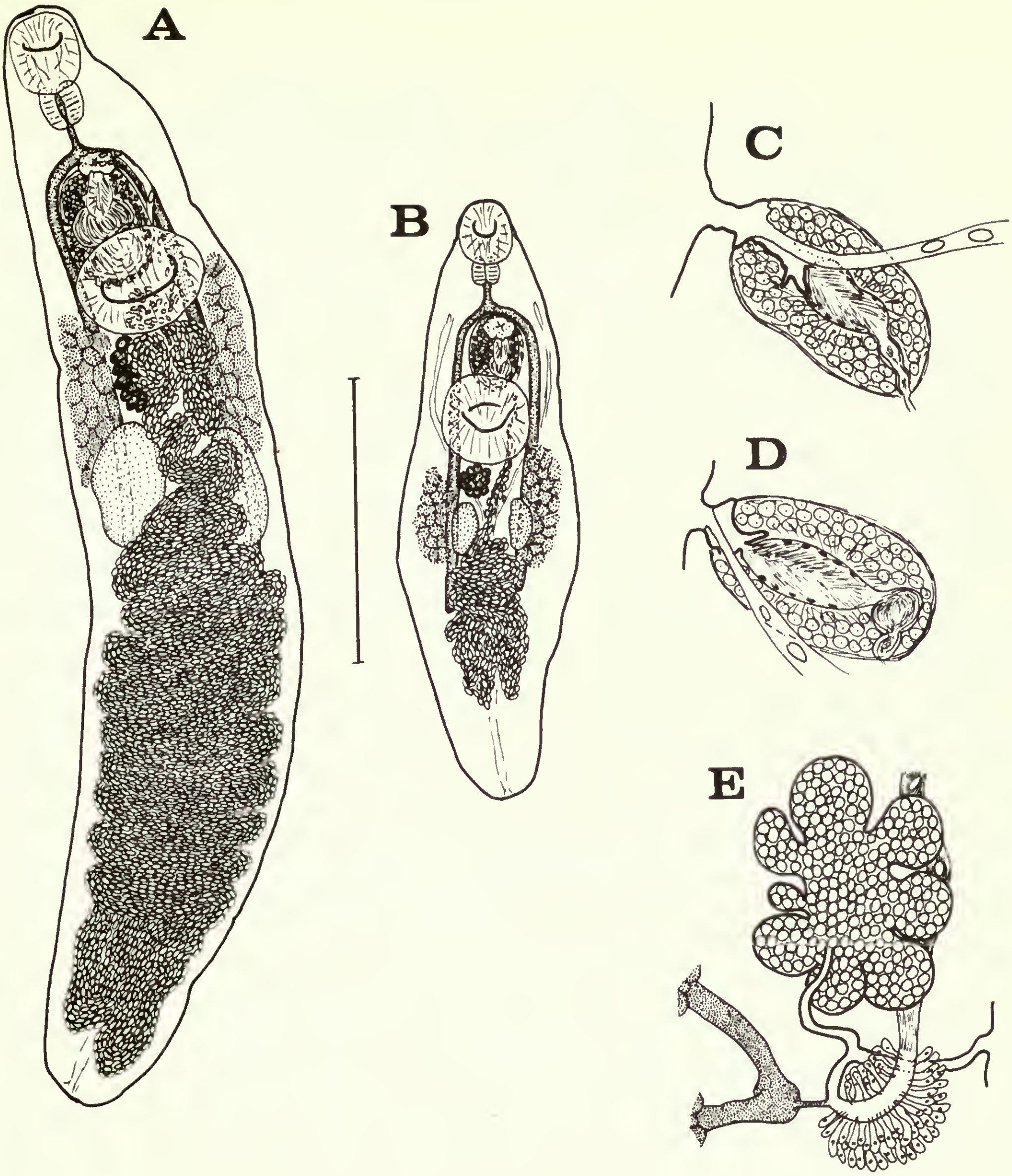


Fig. 3 *Steringophorus furciger*: (a) large specimen from *Reinhardtius hippoglossoides*; (b) early mature specimen from *Hippoglossoides platessoides*; (c) cirrus-sac with almost empty seminal vesicle; (d) cirrus-sac with partly empty seminal vesicle; (e) diagram of female proximal genitalia. Bar scale: a, b = 1 mm.

and its initial loops constitute a uterine seminal receptacle (Fig. 3e). The bulk of the uterus, however, coils in the post-testicular region of the hindbody, but it appears that as the worm ages the part of the uterus between the testes and the ventral sucker also fills with eggs. The uterus passes dorsally to the ventral sucker as a straight, narrow duct and opens into the genital atrium laterally to the cirrus-sac. The numerous eggs have smooth shells, but they may possess a small boss on the anopercular pole. Many worms have some small, deformed eggs; but, with the exception of one specimen from *Lycenchelys sarsi*, all contain some full-sized eggs. The vitelline follicles lie in two

Table 2 Dimensions of *Steringophorus furciger* from the present material and from the literature

Authority	Odhner (1905)	Lebour (1908*a*)	Yamaguti (1934)	Strelkov (1960)	Present material
Hosts	*Gymnacanthus ventralis* *Lycodes pallidus* +Olsson's	Flatfish (5 spp.) *Lophius piscatorius*	*Bothrocara zesta* *Furcimanus nakamurae*	Flatfish (4 spp.) *Theragra chalcogramma*	see text
Locality	E. Greenland, etc.	Northumberland	Japan	E. Kamchatka	see text
Length (mm)	3·5	1·5–3·5	1·87–3·12	2·1–5·0	1·35–4·08
Breadth (mm)	0·6–1·1	–	0·85–1·18	0·8–1·4	0·62–1·16
Length : forebody ratio	(1 : 0·22)	(1 : 0·30)	–	–	1 : 0·18–0·44
Oral sucker (mm)	0·2–0·3	0·2	0·20–0·28 × 0·20–0·32	0·24–0·31	0·14–0·33 × 0·17–0·34
Ventral sucker (mm)	0·35–0·55	0·35	0·28–0·46 × 0·36–0·60	0·49–0·60	0·24–0·56 × 0·23–0·54
Sucker-ratio	1 : 1·7	1 : 1·7	–	–	1 : 1·5–2·3
Pharynx (mm)	–	–	0·10–0·13 × 0·10–0·12	0·14–0·19 × 0·10–0·14	0·10–0·17 × 0·07–0·17
Oesophagus (mm)	0·10–0·13	–	0·05–0·15	–	0·04–0·33
Cirrus-sac (mm)	–	–	0·47–0·32	–	0·17–0·45 × 0·10–0·33
Testes (mm)	–	–	0·25–0·46 × 0·21–0·36	0·27–0·37	0·15–0·37 × 0·11–0·55
Ovary (mm)	–	–	–	0·18–0·30	0·15–0·28 × 0·12–0·38
Eggs (μm)	46–66 × ?	46 × 19	60–68 × 34–36	45–54 × 16–24	42–54 × 23–33

tightly packed lateral fields reaching from the level of the hinder margin of the ventral sucker to a level between the anterior margin of the testes and immediately posterior to the testes. The main vitelline collecting ducts unite ventrally to Mehlis' gland to form a small reservoir which is connected to the oviduct via a short, narrow common duct.

DISCUSSION. There are one or two features of this worm on which there is disagreement in the literature. Levinsen (1881) and Lebour (1908*a*) claim to have seen a distinct seminal receptacle; but we have been unable to trace one in our specimens. We tend to agree with Odhner (1905), who suggested that Levinsen in fact saw just a small inflation of Laurer's canal, possibly a structure which we (Gibson & Bray, 1979) refer to as a 'rudimentary seminal receptacle'. Although we have not seen such a dilation, Lebour (1908*a*) stated that Laurer's canal led from the seminal receptacle (this is clearly shown in her Fig. 7), and Yamaguti (1934) says, 'there is a small receptaculum seminis which may be considered a dilatation of the [*sic*] Laurer's canal'. Linton (1940) also failed to find any structure, other than the uterine seminal receptacle, which acted as a sperm-store in the female part of the reproductive system.

Yamaguti (1934) and Miller (1941) consider that the genital pore is normally medially situated; but Odhner (1905) stated that this is abnormal, and in most of our material the genital pore lies to the left of the median line.

A suspicion that all of the records may not be of the same species is aroused by the reports of egg-sizes well above those found in our specimens and in the majority of specimens described in the literature. Odhner (1905) found that his specimens from *Lycodes pallidus* and *Gymnacanthus tricuspis* had eggs between 60 and 66 μm in length, and Yamaguti's (1934) specimens had eggs of 60 to 68 μm in length. A close examination of further specimens with these large eggs is desirable. Our own specimens from *Lycodes esmarki*, *L. vahli* and *Lycodes* sp. all had eggs between 42 and 50 μm in length.

Steringophorus agnotus (Nicoll, 1909) Dollfus, 1952

Fellodistomum agnotum Nicoll 1909.
Fellodistomum incisum (Rudolphi) of Stafford (1904) in part (?).

TYPE-HOST AND LOCALITY. *Anarhichas lupus*, St Andrews, Fife, Scotland.

RECORDS

(i) Material studied

(a) From the NE Atlantic

Anarhichas lupus [bile-duct] Eldey Bank, off Reykjanes, Iceland (64°N, 24°W; depth 148–152 m; May, 1974). BM(NH) 1977.3.4.1–2.

—— [bile-duct] Moray Firth, Scotland (58°N, 02°W; depth 164 m; July, 1976). BM(NH) 1977.3.4.3.

(b) From elsewhere

Anarhichas lupus [intestine] Newfoundland (see Bray, 1979 : 420). BM(NH) 1977.2.16.55.

(ii) NE Atlantic records from the literature

Anarhichas lupus [gall-bladder & duodenum] St Andrews, Fife, Scotland. Nicoll (1909*a* : 469; as *Fellodistomum agnotum*).

—— [anterior intestine] Trondheim, Norway. Odhner (1911*a* : 99).

—— [bile-duct] Húsavík, Neskaupstadur and Reykjavik, Iceland. Brinkmann (1956 : 22; as *Fellodistomum agnotum*).

Anarhichas minor [gall-bladder] Umîvik, East Greenland. Brinkmann (1975 : 52; as *Fellodistomum agnotum*).

ASPECTS OF BIOLOGY. This parasite is found in anarhichadid fishes in the North Atlantic Ocean and the Barents Sea. It has been confused in the past with *Fellodistomum fellis* (see Dawes, 1947) which occurs in the same host; but it apparently has a slightly different site-preference. While *F. fellis* occurs almost exclusively in the gall-bladder, *S. agnotus* apparently occurs in the duodenum (Polyansky, 1955 : 56), as well as in the bile-duct and gall-bladder. The largest specimen that we found came from the intestine, but our other eight specimens all came from the bile-duct.

The life-history of this species is unknown.

PREVIOUS DESCRIPTIONS Nicoll (1909*a* : 469; as *Fellodistomum agnotum*); Miller (1941 : 43; as *F. agnotum*); Polyansky (1955 : 56; as *F. agnotum*); Brinkmann (1956 : 22; as *F. agnotum*); Srivastava & Ghosh (1968 : 49; as *F. agnotum*).

DESCRIPTION (Fig. 4). Eight whole-mounts and one sectioned specimen were studied. These worms are less robust than *Fellodistomum fellis* (see Table 3 for dimensions). The body is widest at the level of the ventral sucker, the forebody tapering sharply and the hindbody, which in some cases is quite extensive, narrowing more slowly (Fig. 4a & b). The body-surface bears no spines and the body-wall is thin. The subterminal, globular *oral sucker* is smaller than the more or less globular *ventral sucker*, which is situated at about one-third of the body-length from the anterior extremity. The sucker-ratio is 1 : 1·3–1·7. There is a short prepharynx, visible only in sections, which leads into a globular to elongate-oval *pharynx* just less than half of the diameter of the oral sucker. The pharynx leads directly into two wide caeca, which terminate just posteriorly to the testes, although not always symmetrically. The semi-digested remains of blood can often be seen in the lumen of the caeca.

At the posterior extremity the 'Y'-shaped *excretory vesicle* opens via the excretory pore. The vesicle, which lies dorsally to the gonads but ventrally to the caeca, bifurcates at about the level of the right testis. The arms reach almost to the level of the pharynx, becoming more dilate in the forebody.

The oval to elongate-oval *testes* lie obliquely with their longitudinal axes oriented antero-posteriorly. The left testis lies more anteriorly than the right, although in our smallest immature specimen the testes are more or less symmetrical. The vasa efferentia pass through the wall of the

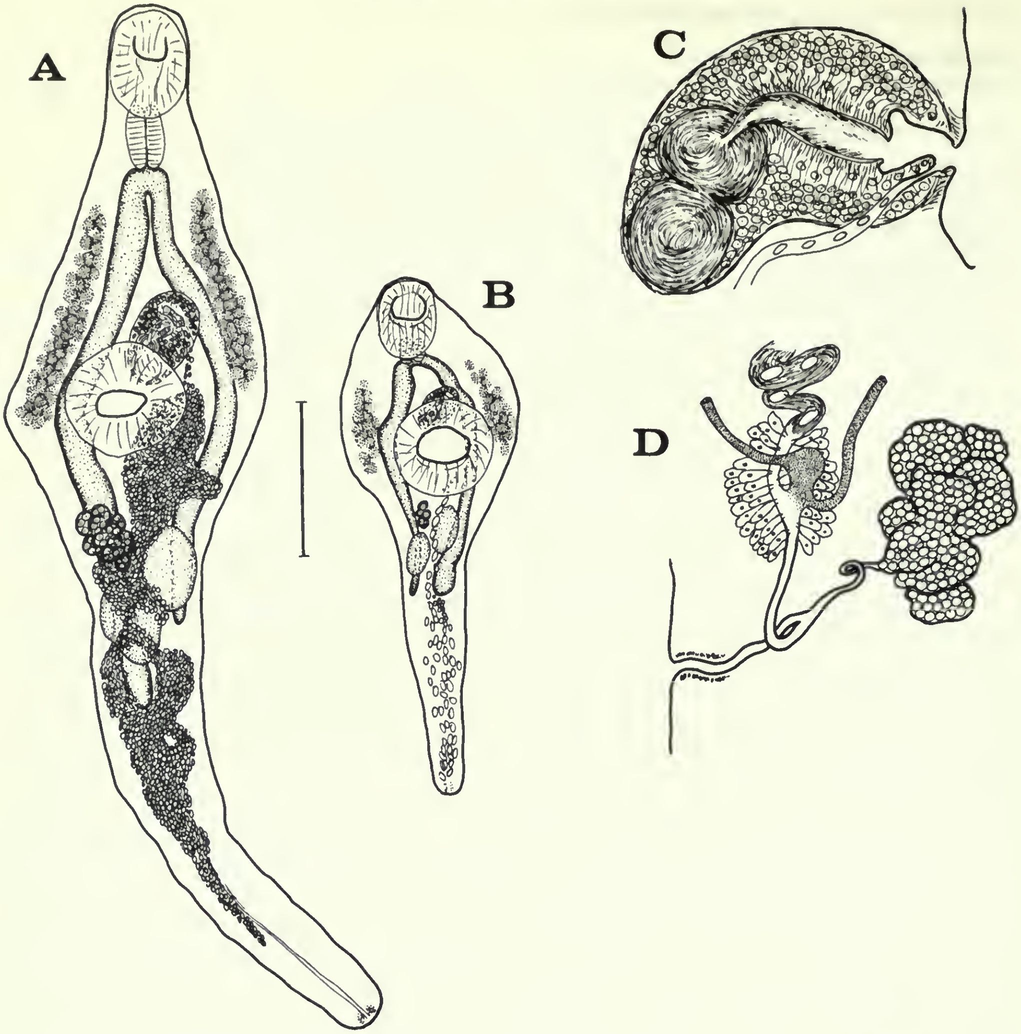


Fig. 4 *Steringophorus agnotus*: (a) specimen from intestine, with small, malformed eggs; (b) small specimen from bile-duct; (c) cirrus-sac; (d) diagram of female proximal genitalia. Bar scale: a, b = 0·5 mm.

cirrus-sac separately, but close together. The *cirrus-sac*, which is present close to the anterior margin of the ventral sucker (Fig. 4c), has a thin muscular wall. It lies at an angle to the body-surface, causing difficulties in accurate measurement in whole-mounts, and contains a bipartite seminal vesicle, a wide pars prostatica surrounded by numerous gland-cells, and a wide ejaculatory duct. The structure of the cirrus-sac and its contents is similar to that of the previous two species, particularly in the filamentous lining of the pars prostatica and the muscular, diverticulate nature of the ejaculatory duct. The genital atrium is small, receiving the female duct from the left side laterally to the cirrus-sac. The genital pore is large, surrounded by an almost sucker-like musculature, and situated to the left of the median line just anteriorly to the ventral sucker.

The multilobate *ovary* lies almost immediately anterior to the right testis. A narrow oviduct passes from its dorsal surface and runs posteriorly to where it unites with Laurer's canal and the common vitelline duct prior to entering Mehlis' gland. In fact the union with the broad common vitelline duct occurs just as the oviduct enters Mehlis' gland. Laurer's canal opens to the exterior at a level just posterior to the ovary (Fig. 4d). There is no seminal receptacle associated with Laurer's canal; but the first few coils of the *uterus* form a uterine seminal receptacle. The uterus is initially coiled just anteriorly to Mehlis' gland, and then coils posteriorly between the testes, reaching close to the posterior extremity. On returning forward it forms a number of coils at the level of the posterior margin of the ventral sucker, before passing anteriorly towards the genital atrium. The terminal region of the uterus which unites with the genital atrium is narrow. The uterus contains numerous 'normal' eggs and often many smaller, apparently malformed, eggs and fragments of vitelline material. The vitelline follicles lie in two lateral fields, reaching from about the level of the middle of the ventral sucker to a level just posterior to the pharynx.

Table 3 Dimensions of *Steringophorus agnotus* from the present material and from the literature

Authority	Nicoll (1909*a*)	Miller (1941)	Srivastava & Ghosh (1968)	Present material
Hosts	*Anarhichas lupus*	*Anarhichas lupus*	*Lophius piscatorius*	*Anarhichas lupus*
Locality	Scotland	Canada	unknown	see text
Length (mm)	up to 3·3	2·9	2·95	1·3–3·4
Breadth (mm)	up to 0·87	1·09	1·25	0·43–0·82
Length : forebody ratio	(1 : 0·36)	(1 : 0·35)	(1 : 0·36)	1 : 0·26–0·41
Oral sucker (mm)	0·34 (in 3 mm specimen)	0·29 dia.	0·31 × 0·36	0·20–0·36 × 0·18–0·26
Ventral sucker (mm)	0·51 (in 3 mm specimen)	0·42	0·45 × 0·49	0·29–0·40 × 0·28–0·41
Sucker-ratio	1 : 1·5	(1 : 1·4)	1 : 1·46	1 : 1·3–1·7
Pharynx (mm)	0·15 × 0·12	0·14 long	0·14 × 0·13	0·097–0·13 × 0·090–0·25
Cirrus-sac (mm)	–	–	–	0·28–0·32 × 0·19–0·22
Testes (mm)	–	–	0·18–0·24 × 0·13–0·20	0·18–0·30 × 0·07–0·17
Ovary (mm)	–	–	0·27 × 0·13	0·13–0·19 × 0·05–0·18
Eggs (µm)	48 × 24	44 × 24	45 × 27	52–61 × 25–29 (+ many malformed)

DISCUSSION. This species exhibits features which are intermediate between *Fellodistomum fellis* and *Steringophorus furciger* both in morphology and biology. It was moved from *Fellodistomum* to *Steringophorus* by Dollfus (1952), on the basis of the extension of the uterus into the post-testicular region, and although it does not appear to have been accepted by any subsequent worker we agree with this move. We have not, however, followed Dollfus in distinguishing these two genera at the subfamily level, as *S. agnotus* is similar to *F. fellis*.

Dawes (1947) considered *Fellodistomum agnotum* to be a synonym of *F. fellis*, but detailed and convincing rebuttals of this have been presented by Polyansky (1955), who lists five distinguishing features, and Brinkmann (1956), who lists ten. Dawes stated, '. . . it is very difficult to conceive of the existence of two distinct species of such rarity and precise host-specificity'. Subsequent work has shown that these species are neither as rare nor as host-specific as Dawes apparently considered them (Brinkmann, 1975). As mentioned above, Yamaguti (1971) regarded *Fellodistomum* as a young form of *Steringophorus* because of the restricted distribution of the uterus in the former, which he suggested varies with age. The extension of the uterus into the post-testicular region of *S. agnotus*, however, is not a sign of maturity, as even the smallest worms have primordia of the uterus in this region.

We have found that in all of our specimens the caeca extend just posteriorly to the testes. Nicoll (1909*a*) and Miller (1941) describe the caeca as reaching the testes, but not going beyond, and in the specimen figured by Srivastava & Ghosh (1968) the caeca did not reach the testes. The latter figure is of a worm which is obviously considerably flattened, and this procedure has probably affected the relative positions of these organs, as is suggested by the median position of the genital pore. It would seem likely that Nicoll's and Miller's (i.e. Stafford's) material may also have been fixed under pressure. Our material was all fixed without pressure in glacial acetic acid. The two specimens studied by Srivastava & Ghosh (1968) were found amongst the slide collection of the late Dr G. S. Thaper and are purported to have been recorded from the gall-bladder of *Lophius piscatorius* from an unknown locality. When the distribution of this host and of the usual host is taken into consideration, it would seem likely that this material came from European or at least northern Atlantic waters. These specimens also differ from other descriptions of *S. agnotus* in appearing to possess a short oesophagus. Brinkmann (1956) uses egg-length as a criterion distinguishing *F. fellis* ('45 µm') and *S. agnotus* ('55 µm'). As Table 3 indicates, this may well be an unsatisfactory character in that some authors have recorded an egg-length in *S. agnotus* similar to that in *F. fellis*. We found that careful examination of eggs lying horizontally *in situ* gave measurements of 52–61 µm. It is most noticeable, however, that many eggs, and in fact all of them in the specimen recovered from the intestine (Fig. 4a), are apparently malformed and much smaller than usual (25–29 µm). The worms from the bile-duct have either a mixture of large and small eggs or large eggs only.

Steringophorus blackeri Bray, 1973

TYPE-HOST AND LOCALITY. *Xenodermichthys socialis* [=*copei*], Bay of Biscay (45°N, 02°W).

RECORDS

(i) Material studied

(a) From the NE Atlantic

Xenodermichthys socialis [intestine & body-cavity] Bay of Biscay (45°N, 02°W; depth 575–665 m; Jan., 1971). Type-material (see Bray, 1973 : 174). BM(NH) 1973.4.9.21–24.

—— [intestine] Porcupine Bank, W. of Ireland (54°N, 14°W; depth 1000 m; June, 1974). BM(NH) 1977.3.15.1.

—— [body-cavity] Rosemary Bank, NW of Scotland (59°N, 10°W; depth 970–1025 m; June, 1974). BM(NH) 1977.3.15.2.

—— [intestine] Flannan region, NW of Scotland (59°N, 09°W; depth 900–940 m; Oct., 1978). BM(NH) 1979.2.14.1.

(b) From elsewhere

Xenodermichthys sp. [intestine] Off Moroccan coast (28°N, 14°W; depth 390 m) (see Bray, 1973 : 174). BM(NH) 1973.5.17.4–5.

(ii) NE Atlantic records from the literature

Xenodermichthys socialis [intestine & body-cavity] Bay of Biscay. Bray (1973 : 174).

ASPECTS OF BIOLOGY. All of the records of this parasite are given above, thus indicating that it has only been found in the alepocephalid genus *Xenodermichthys* from the eastern North Atlantic. The worms are rather large in comparison with the lumen of the intestine, where they normally reside. In many cases they appear to quite effectively block the gut, and, as the wall of the intestine surrounding them is severely stretched, it is easy to imagine them breaking through into the body-cavity, where a number have been found.

PREVIOUS DESCRIPTION. Bray (1973 : 174).

DESCRIPTION (Fig. 5). Thirteen whole-mounted and two sectioned specimens were available for study, the measurements of which are given in Table 4. The shape of the body of these large worms may be broadly oval, especially in specimens from the body-cavity, to elongate-oval,

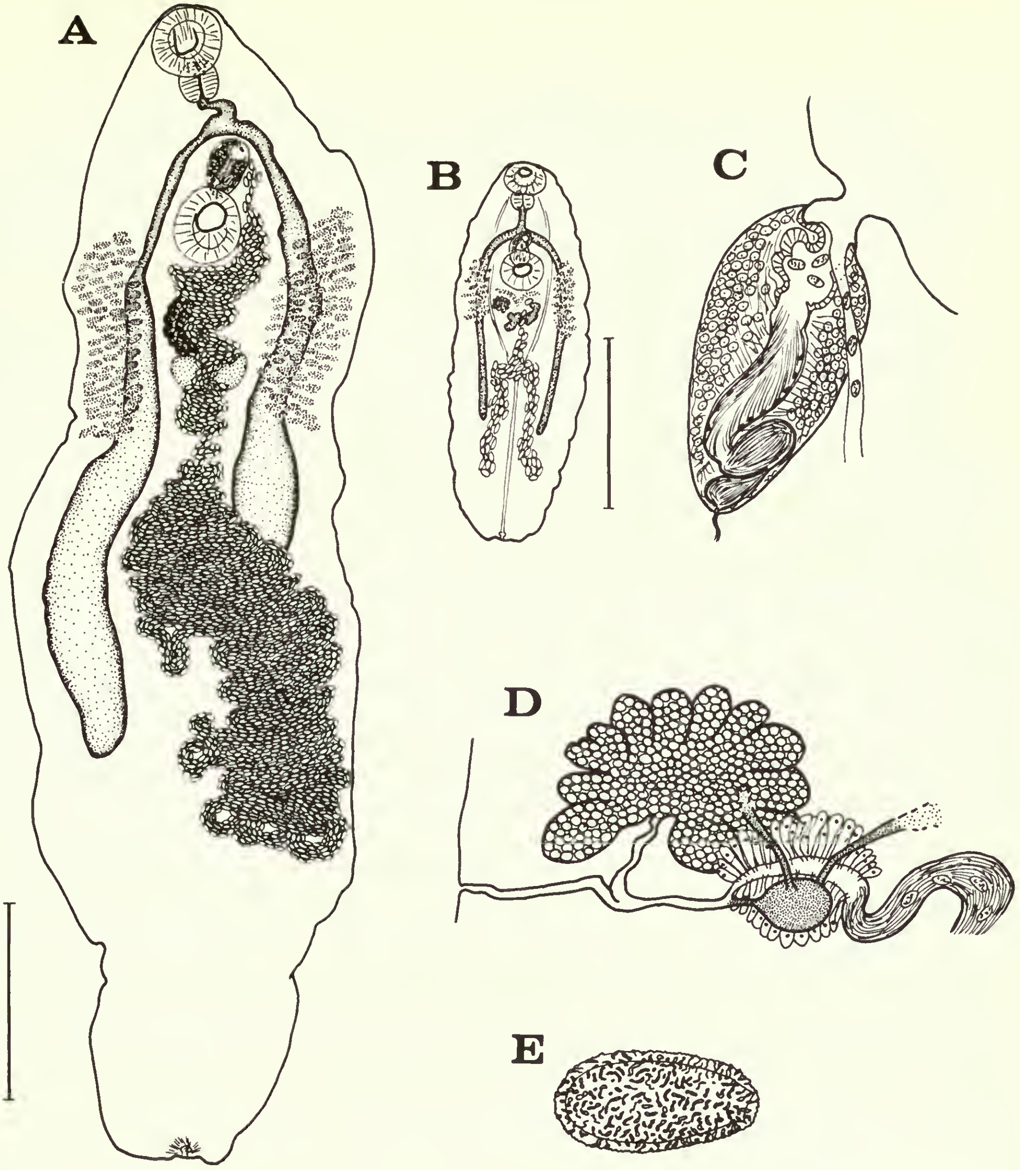


Fig. 5 *Steringophorus blackeri*: (a) large specimen from intestine; (b) small specimen from intestine; (c) cirrus-sac; (d) diagram of female proximal genitalia; (e) egg. Bar scales: a, b = 1 mm.

especially in large specimens from the intestine (Fig. 5a). One specimen is divided into three more or less equal parts by two constrictions, which thus give it a moniliform appearance. The forebody is smaller than the hindbody in the ratio of 1 : 3–6; but with this ratio increasing allometrically with increased length of the worms. The body-surface is smooth. There is a globular, subterminal *oral sucker*, which is similar in size to, but may be slightly smaller or larger than, the globular *ventral sucker*. There is a short prepharynx, a large *pharynx* and a short oesophagus which is surrounded by gland-cells. The intestinal bifurcation, which occurs at about the middle of the forebody, gives rise to caeca which reach posteriorly to about the middle of the hindbody, normally terminating amongst the coils of the uterus. These caeca may be narrow or wide, and are often full of the semi-digested remains of blood.

Table 4 Dimensions of *Steringophorus blackeri* from the present material and from the literature

Authority	Bray (1973)	Present material (collected 1974 & 1978)
Length (mm)	2·2–9·0	3·0–5·95
Breadth (mm)	0·8–2·04	1·20–2·1
Length : forebody ratio	1 : 0·14–0·29*	1 : 0·15–0·27
Oral sucker (mm)	0·24–0·47 dia.	0·30–0·40 × 0·27–0·43
Ventral sucker (mm)	0·24–0·49 dia.	0·27–0·42 × 0·30–0·50
Sucker-ratio	1 : 0·85–1·12	1 : 0·84–1·24
Pharynx (mm)	0·11–0·26 × 0·125–0·32	0·21–0·26 × 0·20–0·26
Oesophagus (mm)	0·105–0·23	0·09–0·17
Cirrus sac (mm)	0·21–0·35 × 0·12–0·19	0·25–0·35 × 0·16–0·23
Testes (mm)	0·07–0·21 × 0·14–0·20	0·20–0·27 × 0·11–0·21
Ovary (mm)	0·18–0·27 × 0·11–0·27	0·18 × 0·13
Eggs (μm)	52–63 × 27–34	48–54 × 26–34

* New data.

The *excretory pore* is terminal and leads into a 'Y'-shaped vesicle, the stem of which may be narrow, especially in specimens from the intestine, or wide and dilate, especially in specimens from the body-cavity. Just posterior to the gonads the vesicle bifurcates, and the arms, which are usually narrow, reach into the forebody to the level of the pharynx.

In young specimens the small, oval *testes* have quite deeply indented margins, but in the larger specimens they are entire. They occur close to each other, almost symmetrically or obliquely with the left testis the more anterior, in the anterior quarter of the hindbody. The vasa efferentia are difficult to follow, but appear to remain separate until after they have passed through the wall of the cirrus-sac. The *cirrus-sac* is oval and tapers slightly at the proximal end (Fig. 5c). It contains a small, bipartite seminal vesicle, a wide, curved pars prostatica with a filamentous lining and a wide, diverticulate ejaculatory duct which may contain eggs. The cirrus-sac and contents are, therefore, typical of this subfamily. The genital atrium is small, receiving the metraterm laterally to the cirrus-sac, and opens via the genital pore just to the left of the median line in the hinder region of the forebody.

Immediately anterior to the right testis lies a multilobate *ovary*. The oviduct leaves this posteriorly and receives Laurer's canal and the common vitelline duct prior to passing into Mehlis' gland (Fig. 5d). Laurer's canal opens dorsally at the level of Mehlis' gland, and often contains small amounts of spermatozoa. A uterine seminal receptacle is the only seminal store in the female part of the reproductive system. Most of the *uterus* lies posteriorly to the gonads: it passes back medially with laterally directed loops to about the middle of the worm, and then descends in a series of loops on one, or more usually on both, sides of the body to about two-thirds of the way down the hindbody. The post-testicular region of the uterus, therefore, often possesses the outline of an inverted 'Y' (Fig. 5b). Anterior to the gonads the uterus tends to pass forward directly to the genital atrium in young specimens, but in the largest specimens it often coils in the region between the gonads and the ventral sucker. There is always a considerable portion of the posterior hindbody devoid of uterine coils. The operculate eggs are variable in size, and the brownish-yellow shells bear a pattern of raised bosses (Fig. 5e). The *vitellarium* consists of two lateral fields of globular or short, transversely-elongate follicles, lying between the anterior margin of the ventral sucker and a level just posterior to the testes. The two fields feed main vitelline ducts which pass medially ventral to Mehlis' gland and unite to form a common vitelline duct. This common duct is dilate proximally, forming a distinct vitelline reservoir.

DISCUSSION. This description extends that of Bray (1973), especially with regard to details of the cirrus-sac, which are corrected here, and the increased range of egg-sizes recorded. With regard to the sucker-ratio, about equal numbers of our specimens possessed a ventral sucker which was either slightly larger or smaller than the oral sucker. Another variable feature is the arrangement of uterine coils in the post-testicular region of the hindbody. The normal arrangement appears to be two lateral coils (Fig. 5b), but occasionally the uterus develops down one side of the body only (Fig. 5a). The difference in body-shape between specimens from the body-cavity and those from the intestine appears to be caused by differences in the dilation of the excretory vesicle. In specimens from the body-cavity the vesicle is wide, this possibly being caused by differences in the osmolarity of the two environments or by other factors, such as the health of the host, which might have upset the normal osmotic balance of these worms. The health of the fish may suffer when these worms pass through the gut-wall.

Steringophorus pritchardae (Campbell, 1975) n. comb.

Abyssotrema pritchardae Campbell, 1975.

TYPE-HOST AND LOCALITY. *Alepocephalus agassizi*, Hudson Canyon, NW Atlantic.

RECORDS

(i) Material studied

(a) From NE Atlantic

Alepocephalus bairdii [upper intestine] Porcupine Bank, W of Ireland (54°N, 14°W; depth 1000–1050 m; June, 1974). BM(NH) 1977.5.23.1–4.

—— [upper intestine] South Rockall, W of Scotland (55°N, 17°W; depth 821–850 m; June, 1974). BM(NH) 1977.5.23.5–6.

—— [upper intestine] Rosemary Bank, NW of Scotland (59°N, 10°W; depth 680–760 m; June, 1974). BM(NH) 1977.5.23.7–8.

—— [pyloric caeca] Sula Sgeir, NW of Scotland (60°N, 07°W; depth 900 m; June, 1974). BM(NH) 1977.5.23.9.

—— [intestine] Sula Sgeir region, NW of Scotland (59°N, 08°W; depth 1160–1220 m; Oct., 1978). BM(NH) 1979.2.14.2.

—— [intestine] Flannan region, NW of Scotland (59°N, 09°W; depth 1000 m; Oct., 1978). BM(NH) 1979.2.14.3.

(b) From elsewhere

Alepocephalus agassizi [intestine] Hudson Canyon, NW Atlantic (39°N, 71°W; depth 1919–2297 m (see Campbell, 1975 : 661).

(ii) NE Atlantic records from the literature

None

ASPECTS OF BIOLOGY. This species has been found only in *Alepocephalus* spp. in the NW and NE Atlantic in deep water down to nearly 2300 m. Campbell (1975) found 247 specimens in 20 *A. agassizi* with 100% incidence. This contrasts with the rate of infestation found in the NE Atlantic where the most found in any one specimen of *A. bairdii* was 6, and the rate of incidence was about 50%. On one occasion this species was found sympatric with *Olssonium turneri*. Spermatophores have been observed by Campbell (1975).

PREVIOUS DESCRIPTION. Campbell (1975 : 661; as *Abyssotrema pritchardae*).

DESCRIPTION (Fig. 6). This description is based on 25 specimens, two of which have been serially sectioned, from the NE Atlantic; and two whole-mounted and two sectioned specimens from the NW Atlantic. The worms are long, narrow, dorsoventrally flattened and bear a small protrusion at the posterior end of the body (Fig. 6a–c).

The dimensions of this species are summarized in Table 5. The body-surface is smooth, and the large *oral sucker* has a longitudinally elongate subterminal opening. It is slightly wider than the globular *ventral sucker*, which lies just inside the anterior quarter of the body. A short prepharynx leads into a small, globular *pharynx*, which, in turn, leads into a long oesophagus that extends back to about the level of the genital pore. At this point the gut bifurcates, giving rise to two

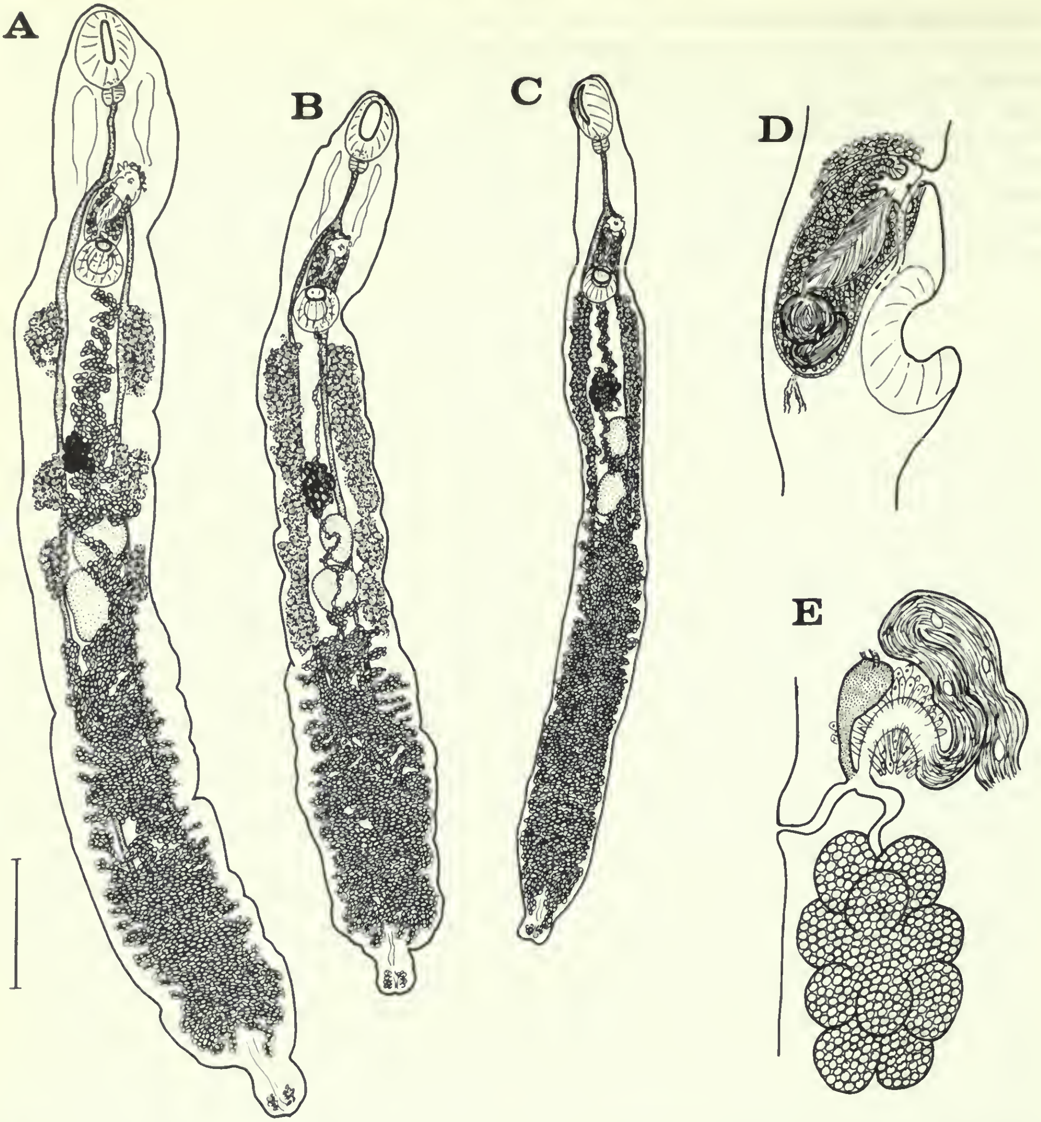


Fig. 6 *Steringophorus pritchardae*: (a–c) wholemount specimens, ventral view; (d) cirrus-sac; (e) diagram of female proximal genitalia. Bar scale: a–c = 1 mm.

narrow caeca which reach back to about the middle of the post-testicular region, where they end blindly.

The *excretory pore* lies at the posterior end of the body surmounted on a distinct protrusion. The initial part of the stem of the 'Y'-shaped vesicle is short, narrow, tubular and surrounded by numerous gland-cells. The main part of the stem is much wider and reaches forward to the level of the middle of the post-testicular region (approximately just anterior to the posterior limit of the gut-caeca), where it bifurcates and gives rise to two arms. These arms are quite wide and extend forward to about the level of the posterior margin of the oral sucker.

The two *testes* are oval, or irregularly oval, and lie in tandem in about the middle of the worm. The posterior testis is often slightly larger than the anterior testis. The vasa efferentia remain separate until close to the wall of the cirrus-sac; but it was not possible to ascertain whether or not they unite just outside it. The *cirrus-sac* is large, elongate-oval and its proximal region lies dorsal to the ventral sucker. It contains a bipartite seminal vesicle, either part of which may be the larger. The pars prostatica, which is surrounded by numerous gland-cells and has a filamentous lining, is wide and thus resembles that of other fellodistomines. The ejaculatory duct is also wide, but it is also muscular and distinctly pocketed. The genital atrium is small, and opens through the genital pore just to the left of the median line and just posterior to the middle of the forebody. Spermatophores may be present on the surface close to the genital pore. There is a sheath of gland-cells present lying across the anterior margin of the cirrus-sac (Fig. 6d).

Table 5 Dimensions of *Steringophorus pritchardae* from the present material and from the literature

Authority	Campbell (1975)	Present material
Host	*Alepocephalus agassizi*	*Alepocephalus bairdii*
Locality	NW Atlantic	NE Atlantic
Length (mm)	3·9–13·8	3·7–9·0
Breadth (mm)	1·1–3·8	0·44–1·2
Length : forebody ratio	(1 : 0·21)	1 : 0·17–0·27
Oral sucker (mm)	0·39–0·67 × 0·37–0·75	0·29–0·57 × 0·21–0·47
Ventral sucker (mm)	0·32–0·67 × 0·30–0·68	0·20–0·46 × 0·19–0·43
Sucker-ratio	1 : 0·85–0·94	1 : 0·91–0·94
Pharynx (mm)	0·21–0·34 dia.	0·08–0·19 dia.
Oesophagus (mm)	0·18–0·51	0·13–0·61
Cirrus-sac (mm)	0·62–1·2 × 0·32–0·55	0·30–0·78 × 0·13–0·25
Testes (mm)	0·37–0·69 × 0·25–0·68	0·16–0·63 × 0·17–0·42
Ovary (mm)	0·23–0·67 × 0·23–0·48	0·19–0·34 × 0·16–0·39
Eggs (μm)	46–53 × 25–29	44–50 × 23–32

Antero-dextrally to the testes lies a multilobate *ovary*, which may or may not be separated from the testes by coils of the uterus. Mehlis' gland is present just anterior to the ovary, and prior to reaching it the oviduct receives Laurer's canal and the common vitelline duct (Fig. 6e). Laurer's canal opens dorsally at the level of the ovary. The initial coils of the *uterus* form a large uterine seminal receptacle, which lies immediately anterior to the ovary and then passes back laterally to the testes. The remainder of the uterus, containing numerous operculate eggs with smooth shells, fills most of the post-testicular region of the hindbody. It initially passes back close to the posterior extremity and then runs forward forming transverse loops which reach close to the lateral margins of the body. At the level of the gonads the uterus becomes confined to the inter-caecal region, and, after passing dorsally to the ventral sucker, it enters the genital atrium from the left side through a muscular metraterm. The *vitellarium* consists of two lateral fields of many small follicles, which extend from about the level of the posterior margin of the posterior testis to the posterior margin of the ventral sucker. In one of the larger specimens these fields are broken up into three quite widely separated groups (Fig. 6a). The main lateral vitelline ducts unite close to Mehlis' gland, forming the common vitelline duct which is dilate proximally and acts as a vitelline reservoir.

DISCUSSION. A comparison of our material from the NE Atlantic with that of Campbell (1975) leaves no doubt that they belong to the same species. There are, however, minor differences between our material and Campbell's description; but these can be explained by differences in interpretation and fixation techniques. Campbell, for example, describes spines in the genital atrium, and has illustrated them for us (Campbell, in litt.): we believe, however, that they are not in fact spines, but hyaline filamentous structures formed initially as a lining of the pars prostatica and which act as precursors of the wall of the spermatophore. These filamentous structures, which often extend from the pars prostatica, through the ejaculatory duct and into the genital atrium, are essentially the same in all of the fellodistomines. Our material also differs in configuration of the uterus, in that the uterine coils overlie the caeca in the post-testicular region. It seems that the inter-caecal condition reported by Campbell is an artifact produced by flattening the worms during fixation, as Campbell's sectioned material shows the uterus extending ventrally to the caeca in the post-testicular region.

Steringophorus thulini sp. nov.

TYPE-HOST AND LOCALITY. *Onogadus argentatus*, N of Rona, Scotland (60°N, 06°W).

RECORDS

(i) Material studied

(a) From NE Atlantic

Onogadus argentatus [intestine] N of Rona, Scotland (60°N, 06°W; depth 1090–1110 m; April, 1973). BM(NH) (Holotype) 1977.3.16.1. (Paratypes) 1977.3.16.2–5.

Rhinonemus cimbrius [intestine] Mid-Skagerrak, between Denmark & Sweden (Dec., 1970). Material of J. Thulin.

Trachyrincus trachyrincus [rectum] St Kilda region, Scotland (58°N, 10°W; depth 1300–1330 m; Oct., 1978). BM(NH) 1979.2.14.4–6.

(b) From elsewhere

None

(ii) NE Atlantic records from the literature

None

ASPECTS OF BIOLOGY. Nothing is known about the biology of this species, except that it occurs in the intestine of gadoids. *S. furciger* is the only other species of the genus purported to occur in gadoids from the NE Atlantic, but it appears likely that these records are questionable or accidental.

PREVIOUS DESCRIPTIONS

None.

DESCRIPTION (Fig. 7). Five specimens from *O. argentatus*, three were serially sectioned after being measured, three from *T. trachyrincus*, one was sectioned, and one specimen from *R. cimbrius* were studied. The worms are fusiform when young (Fig. 7b), but the hindbody widens allometrically in older worms (Fig. 7a, c). The body-surface is smooth. Both suckers are globular, and, as can be seen from the dimensions of this species given in Table 6, the subterminal *oral sucker* is consistently slightly smaller than the *ventral sucker*, which lies at about one-third of the body-length from the anterior end. A short prepharynx (seen only in sections), a globular *pharynx* and a distinct oesophagus form the anterior part of the alimentary system. In about the middle of the forebody the intestine bifurcates and the narrow caeca extend back to about the middle of the post-testicular region.

The *excretory pore* is terminal and leads into a 'Y'-shaped vesicle, the stem of which forms a flattened sac. At the testicular level it divides, forming two wide arms which reach into the forebody approximately to the level of the pharynx.

The large *testes* lie symmetrically in the anterior half of the hindbody. They have deeply indented margins. The vasa efferentia pass separately, but close together through the wall of the cirrus-sac. The oval *cirrus-sac* is present in the posterior region of the forebody slightly overlapping the anterior margin of the ventral sucker. It normally contains a large bipartite seminal vesicle, wide pars prostatica with filamentous lining and short, wide, pocketed ejaculatory duct (Fig. 7d). In one sectioned specimen, however, the ejaculatory duct is apparently everted and the contents of the cirrus-sac are distorted. The seminal vesicle of this worm is almost empty and, although it gives the appearance of being bipartite, it is not easy to distinguish where the pars prostatica begins. It would appear, however, that the most distal part of the duct is probably the

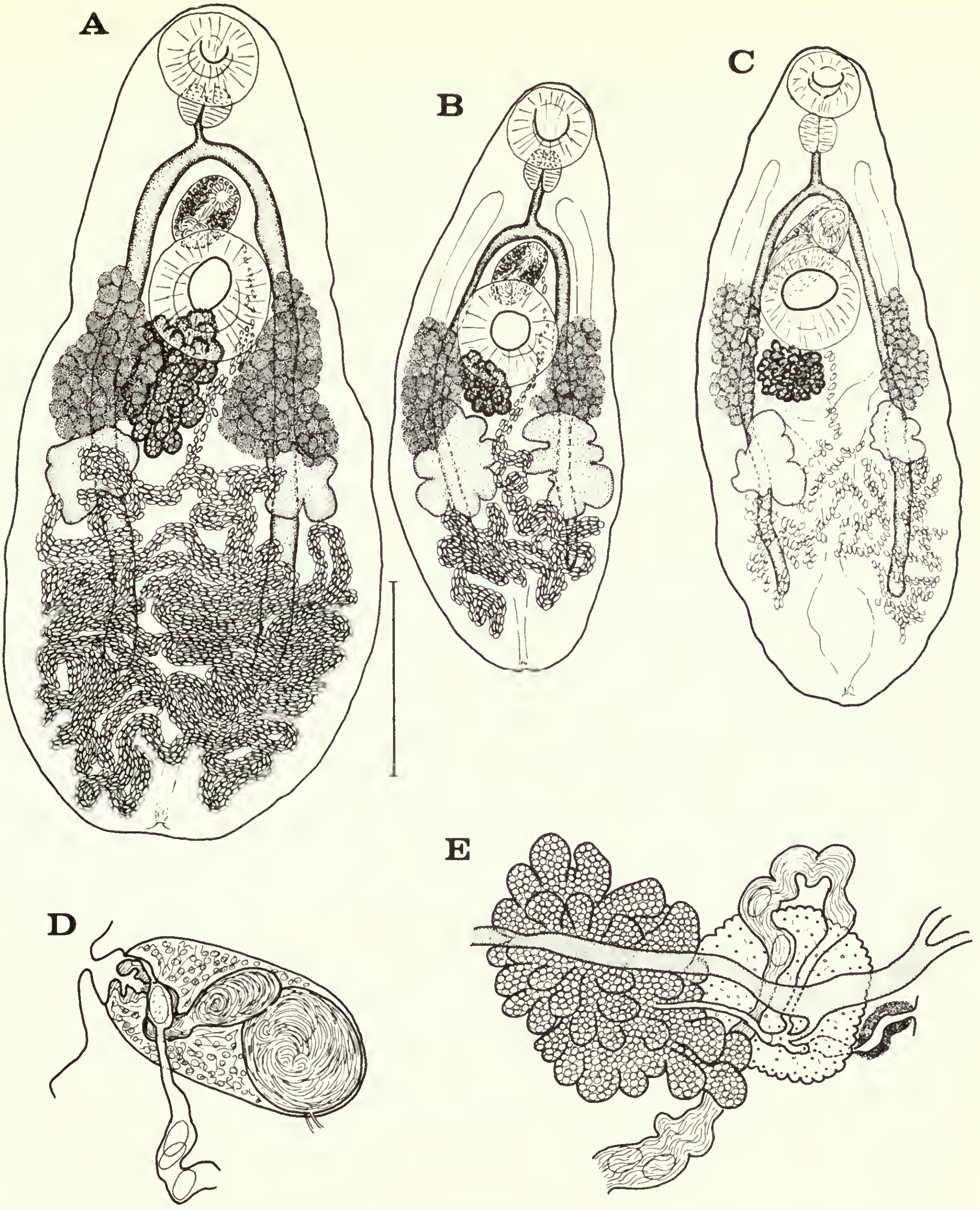


Fig. 7 *Steringophorus thulini*: (a & b) specimens from *Onogadus argentatus*; (c) specimen from *Trachyrincus trachyrincus*; (d) cirrus-sac; (e) diagram of female proximal genitalia. Bar scale: a, b, c = 0·5 mm.

pars prostatica, as the prostatic cells appear to arise from this region. There is little evidence of the ejaculatory duct, and we must assume that it has become the external wall of the genital papilla or cirrus. It seems likely that this specimen has ejaculated shortly prior to being fixed, and that the missing filamentous lining to the pars prostatica probably formed the wall of the spermatophore. The genital atrium is normally larger than is usual in this subfamily, and possesses a wide pore lying slightly sinistrally immediately posterior to the intestinal bifurcation.

Table 6 Dimensions of *Steringophorus thulini*

Host	*Onogadus argentatus*	*Rhinonemus cimbrius*	*Trachyrincus trachyrincus*
Locality	Scotland	Skagerrak	Scotland
Length (mm)	1·46–2·15	1·65	1·7–1·85
Breadth (mm)	0·60–1·00	0·90	0·74–0·86
Length : forebody ratio	1 : 0·26–0·34	1 : 0·42	1 : 0·27–0·31
Oral sucker (mm)	0·16–0·24 × 0·18–0·24	0·20 × 0·22	0·16–0·18 × 0·16–0·21
Ventral sucker (mm)	0·21–0·33 × 0·21–0·32	0·22 × 0·26	0·24–0·30 × 0·28–0·30
Sucker-ratio	1 : 1·2–1·3	1 : 1·1	1 : 1·43–1·75
Pharynx (mm)	0·099–0·124 × 0·103–0·128	0·12 × 0·09	0·07–0·11 × 0·09–0·11
Oesophagus (mm)	0·065–0·103	0·15	0·10–0·14
Cirrus-sac (mm)	0·16–0·23 × 0·14–0·15	*c.* 0·19 × 0·11	0·24–0·32 × 0·13–0·14
Testes (mm)	0·18–0·28 × 0·20–0·28	0·19–0·23 × 0·19–0·25	0·18–0·27 × 0·16–0·20
Ovary (mm)	0·17–0·27 × 0·20–0·40	*c.* 0·23 dia.	0·19–0·22 × 0·24–0·29
Eggs (μm)	36–43 × 20–23 (usually 38–42 × 20–22)	42–43 × 21–24	37–47 × 18–22 (usually 38–41 × 20–22)

The large, multilobate *ovary* lies antero-medially to the right testis, and may be overlapped anteriorly by the posterior margin of the ventral sucker. A large, prominent Mehlis' gland lies to the left of the ovary and, just prior to entering it, the oviduct receives Laurer's canal and the common vitelline duct (Fig. 7e). Laurer's canal follows a convoluted course and opens dorsally at about the level of the ovary. There is no seminal storage organ associated with Laurer's canal, but the proximal end of the *uterus* forms a uterine seminal receptacle. The bulk of the narrow, convoluted uterus, which contains numerous smooth-shelled, operculate eggs, occupies most of the post-testicular region of the hindbody in the form of a mass of convoluted tubules that extends extra-caecally. The last coils are inter-testicular, after which it passes forward directly towards the genital atrium which it enters laterally through a narrow metraterm. The *vitellarium* consists of two lateral fields of closely packed follicles lying between the middle of the ventral sucker and the anterior margin of the testes and often overlapping the caeca ventrally. The follicles feed two main lateral collecting ducts which unite to form a common duct just ventrally to Mehlis' gland.

Discussion. This species is most similar to *S. foliatus* (Yamaguti, 1970) comb. nov., from the intestine of *Emmelichthyops* sp. off Hawaii, for which Yamaguti (1970) created the new genus *Callodistomoides*. It can, however, be distinguished from this species by its shorter caeca, smaller eggs and slightly larger vitelline field.

The specimens from *T. trachyrincus* show slight differences from those in the other hosts. The cirrus-sac is consistently larger and the sucker-ratio is greater. These do not appear to be features which would make it necessary to consider them as belonging to a different species. In the collections of the British Museum (Natural History) there is a similar mature worm from *Lepidion eques* in Newfoundland (BM(NH) 1967.6.19.1, collected by W. Templeman). It has a sucker-ratio of 1 : 2·1 and the only undeformed egg is 48 × 22 μm. An immature specimen has a sucker ratio of 1 : 1·7.

We have named this species in honour of Mr Jan Thulin, University of Gothenburg, Sweden, as an expression of thanks for all the help which he has given us by providing material from his collections, both of this group and others in the series.

Genus *OLSSONIUM* gen. nov.

Definition. Body small; fusiform. Body-surface smooth. Oral sucker subterminal; globular. Ventral sucker in anterior half of body; similar in size to oral sucker. Prepharynx small but distinct. Pharynx small. Oesophagus short. Caeca narrow; reaching almost to testes. Testes oval;

more or less symmetrical; in anterior hindbody. Cirrus-sac large; containing bipartite seminal vesicle, wide pars prostatica with filamentous lining and external gland-cells, and wide, diverticulate ejaculatory duct. Genital atrium large. Genital pore ventral in posterior forebody; slightly sinistral. Ovary trilobed; anterior to right testis and postero-dextral to hind margin of ventral sucker. Laurer's canal and uterine seminal receptacle present. Uterus coils in post-testicular region, in inter-testicular region and dorsally to ventral sucker. Eggs small; operculate; with smooth shell, but may have small boss at one or both ends. Vitellarium follicular; in two lateral fields in forebody. Excretory vesicle 'Y'-shaped; with wide stem bifurcating at level of testes to give rise to two dilate arms which extend into forebody. Parasitic in intestine of marine teleosts.

TYPE-SPECIES. *Olssonium turneri* sp. nov.

COMMENT. This genus differs from *Steringophorus* notably in the distribution of the vitellarium and the shape of the ovary. Other similar fellodistomid genera which possess a 'Y'-shaped excretory vesicle are *Hypertrema* Manter, 1960, *Pseudosteringophorus* Yamaguti, 1940, and *Benthotrema* Manter, 1934. *Hypertrema* has a double egg-shell and a cirrus-sac which is often constricted in the middle, the distal part being bulbous and containing the ejaculatory duct, pars prostatica and one section of the tripartite seminal vesicle. The narrower proximal portion contains two further sections of the seminal vesicle (Overstreet & Martin, 1974). The vitelline fields unite medially in the forebody and the ovary, which consists of three rounded and distinctly separate parts ('ovaries 3' – Overstreet & Martin, 1974), lies medially to the right testis. *Hypertrema* is also said to possess a large, muscular papilla in the genital atrium, but this may be part of the ejaculatory duct, as described in other fellodistomines. Bilqees (1976) considers her new genus *Pseudohypertrema* to be similar to *Hypertrema*. Unfortunately, the shape of the excretory vesicle of *Pseudohypertrema* was not described; but it differs from *Olssonium* in a number of features, notably the double-shelled nature of the eggs, the inter-testicular and sub-globular ovary, the confluent vitelline fields, the caeca extending into the post-testicular region and the morphology of the cirrus-sac. *Pseudosteringophorus* has an oval ovary, a single vitelline field, a long oesophagus and a thin-walled cirrus-sac; but it is obviously similar to *Olssonium*. *Benthotrema* is also similar, especially when the species added to the genus by Yamaguti (1938) and Manter (1954) are considered. Manter (1934) did not describe the excretory vesicle, but the later reports indicate that it is 'Y'-shaped. It differs from *Olssonium*, however, in having an oval ovary and, usually, a coiled seminal vesicle. *Benthotrema hoplognathi* Yamaguti, 1938, which has a bipartite seminal vesicle, differs, in addition to the oval ovary, in the apparent presence of a distinct seminal receptacle, a more lateral position of the genital pore and in the apparent absence of a wide, diverticulate ejaculatory duct. As this species is superficially similar to *Olssonium* and as there are certain questionable features in Yamaguti's description, e.g. the presence of a distinct seminal receptacle, it is possible that a future study of this species might show that it belongs in *Olssonium*. *Benthotrema hilsii* Zaidi & Khan, 1977, may be a species of *Faustula* Poche, 1926, many species of which have been recorded from the same host.

This genus is named in honour of the nineteenth century Scandinavian helminthologist Dr Peter Olsson, who did much valuable work on the parasites of marine fishes.

Olssonium turneri sp. nov.

TYPE-HOST AND LOCALITY. *Alepocephalus bairdii*, W of Ireland (54°N, 14°W).

RECORDS

(i) Material studied

(a) From the NE Atlantic

Alepocephalus bairdii [Upper intestine] Porcupine Bank, off western coast of Ireland (54°N, 14°W; depth 1000 m; June, 1974). BM(NH) (holotype) 1977.3.17.1 (paratype) 1977.3.17.2.

(b) From elsewhere

None

(ii) NE Atlantic records from the literature
None

ASPECT OF BIOLOGY: This species was found sympatrically with *Steringophorus pritchardae*.

PREVIOUS DESCRIPTIONS. None.

DESCRIPTION (Fig. 8). Only two specimens were found, one of which (the paratype) was studied in serial section. Most of the measurements were taken from the single wholemount, which is

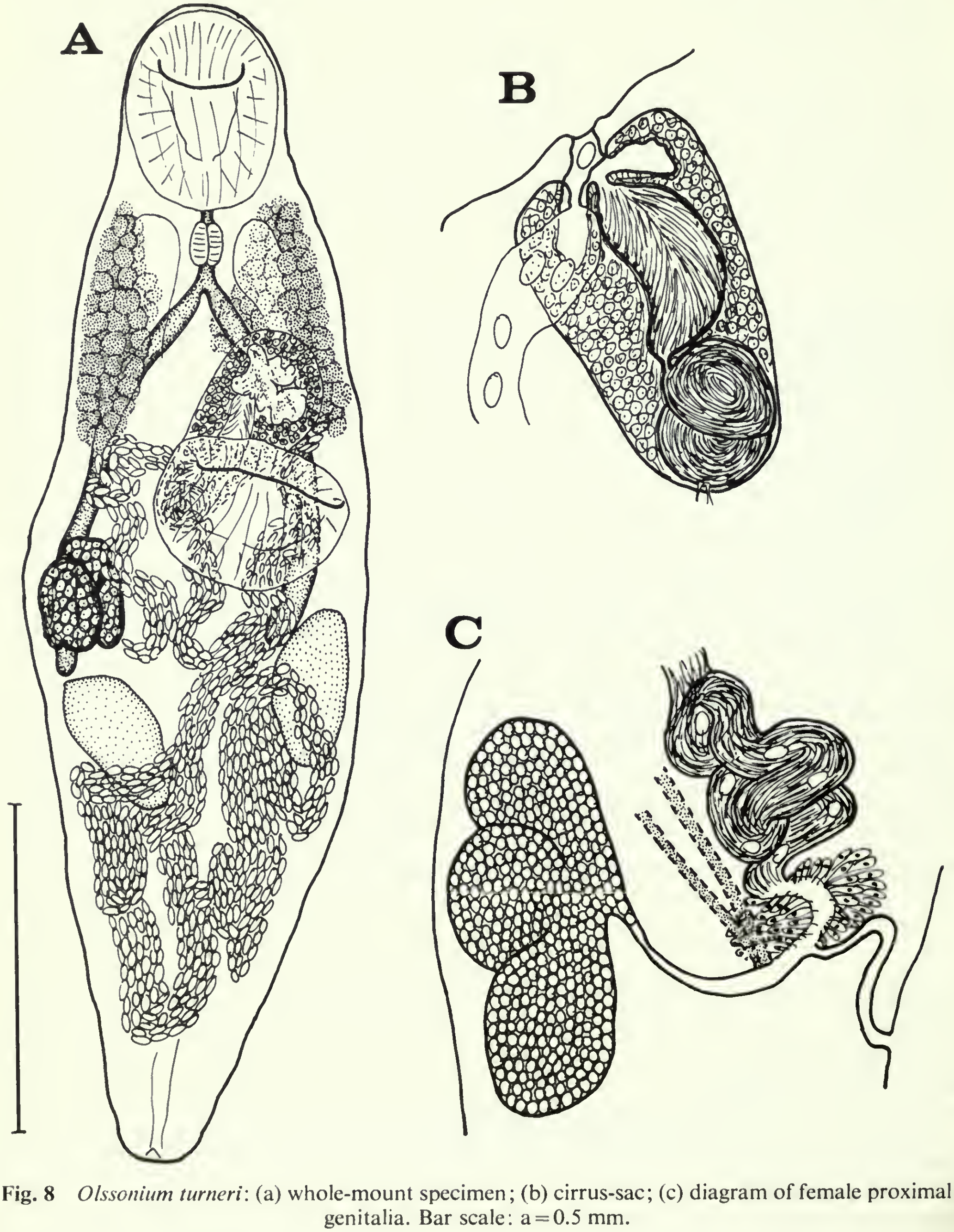


Fig. 8 *Olssonium turneri*: (a) whole-mount specimen; (b) cirrus-sac; (c) diagram of female proximal genitalia. Bar scale: a = 0.5 mm.

2·02 mm long and 0·53 mm wide at its widest point just posterior to the ventral sucker. The worm is fusiform with bluntly rounded extremities (Fig. 8a), and the body-surface is smooth. The *oral sucker* (0·29 × 0·23 mm) opens just subterminally, and is similar in size to the *ventral sucker* (0·22 × 0·29 mm), which lies just inside the anterior half of the body. The length/forebody ratio is 1 : 0·37. There is a short (0·01 mm) but distinct prepharynx which opens into a small *pharynx* (0·07 × 0·057 mm). The oesophagus is short (0·04 mm) and gives rise, in about the middle of the forebody, to two narrow caeca. These reach back approximately to the level of the anterior margin of the testes.

The *excretory pore* is terminal and leads into the wide stem of a 'Y'-shaped excretory vesicle. The stem divides at about the level of the testes, and the arms reach to the level of the pharynx, being dilate in the forebody.

The oval *testes* (0·23–0·24 × 0·11–0·13 mm) are almost symmetrically arranged, but the right testis is slightly more posterior, and the longest axis is oriented longitudinally. The vasa efferentia pass separately, but close together through the wall of the cirrus-sac. The *cirrus-sac* (0·32 × 0·18 mm) is of the typical fellodistomine type and overlaps the anterior margin of the ventral sucker. It contains a bipartite seminal vesicle, a wide pars prostatica with a filamentous liningand a wide, diverticulate ejaculatory duct, all of which are surrounded by the external gland-cells of the pars prostatica (Fig. 8b). The genital atrium is small and opens ventrally, through the genital pore, just to the left of the median line in the posterior half of the forebody.

The distinctly tri-lobed *ovary* (0·20 × 0·13 mm) is situated just anteriorly to the right testis, postero-laterally to the ventral sucker, and ventral to the right caecum. The oviduct leaves the ovary dorsally and passes towards the dorsal surface where it enters a rather amorphous Mehlis' gland. The sectioned specimen is distorted by a dorsal invagination, but it appears that prior to reaching Mehlis' gland the oviduct receives Laurer's canal and probably the common vitelline duct, although this was not seen. Laurer's canal is short and curves between its union with the oviduct and its pore which opens dorsally just posterior to Mehlis' gland (Fig. 8c). The proximal *uterus* forms a large, tightly coiled uterine seminal receptacle. The remainder of the uterus extends well into the post-testicular region, and also lies between the testes, in the pre-testicular region of the hindbody and dorsally to the ventral sucker. It joins the genital atrium from the left side via a short, narrow duct which forms the end of the wide, thin-walled metraterm. The numerous, operculate eggs (38–42 × 24–25 µm), which sometimes bear small bosses at one or both poles, have otherwise smooth shells. There are two lateral fields of tightly packed *vitelline follicles* which occur in the forebody between the anterior margin of the ventral sucker and the posterior margin of the oral sucker. They surround the arms of the excretory vesicle ventrally, laterally and dorsally. Although the left field may lie dorsally to part of the cirrus-sac the two fields do not unite medially.

DISCUSSION. It is unfortunate that the specimen chosen for sectioning was distorted in the region of the female proximal system. Much of the system could be made out, but the exact nature of the junction of the vitelline system with the oviduct was not seen.

This species is named in honour of Mr Robert J. 'Bob' Turner, of the MAFF Laboratory at Lowestoft in gratitude for his help to one of us (R. A. B.) on numerous occasions.

Genus ***STERINGOTREMA*** Odhner, 1911

Rhodotrema Odhner, 1911.

Yamaguti (1953*a*) points out that *Rhodotrema* has page-priority over *Steringotrema*, but suggests that as the type-species of *Rhodotrema* [*R. ovacutum* (Lebour, 1908)] is based on an immature worm, *Steringotrema* should be given preference. *R. ovacutum*, however, is not in fact based on an immature worm (see Lebour, 1908*b*); but for the sake of stability we are invoking Article 24(a) of the International Code of Zoological Nomenclature, crediting Yamaguti (1953*a*) as being the 'first reviser', and, therefore, retaining the name *Steringotrema* for this genus.

DIAGNOSTIC FEATURES. Body small to large; globular to oval. Body-surface smooth. Oral sucker globular to oval. Ventral sucker large; significantly larger than oral sucker; globular; in middle of worm. Prepharynx short. Pharynx well developed. Oesophagus short. Caeca extend back to level of testes or just beyond. Testes two; symmetrical; post-ovarian; in anterior hindbody. Cirrus-sac oval. Seminal vesicle bipartite. Pars prostatica wide; with filamentous lining. Ejaculatory duct wide; diverticulate. Genital atrium small. Genital pore median to sinistrally submedian; at about level of caecal bifurcation. Spermatophores may be present. Ovary entire to trilobate; just anterior or antero-median to right testis. Uterus mainly post-testicular; fills most of hindbody in older specimens. Eggs numerous; operculate; often with considerable variation in size; occasionally with ornamented shells. Vitellarium follicular; in two or four lateral fields between mid-forebody and level of testes; occasionally confluent dorsally. Excretory vesicle 'V'-shaped; arms reaching to pharynx. Parasitic in intestine (occasionally gall-bladder and stomach) of marine teleosts.

TYPE-SPECIES. *Steringotrema pagelli* (van Beneden, 1871) (syn. *S. cluthense* (Nicoll, 1909) – type by original designation).

COMMENT. We have not been able to find any good reason to accept *Rhodotrema* Odhner, 1911, as a valid genus distinct from *Steringotrema*. The characters which differentiate the type-species, *R. ovacutum* (Lebour, 1908), from other species of *Steringotrema* are given in the key presented below; these differences, in our opinion, do not warrant a generic distinction. The genus *Rhodotrema* has, however, been credited with a number of species in the past; but it is apparent that the following species should be considered species, or synonyms of species, of the opecoelid genus *Stenakron* Stafford, 1904, and related genera (see p. 201 and Bray, 1979):

1. *Rhodotrema problematicum* Issaitschikov, 1928
2. *Rhodotrema skrjabini* Issaitschikov, 1928
3. *Rhodotrema quinquelobatum* Layman, 1930
4. *Rhodotrema quadrilobatum* Bazikalova, 1932
5. *Rhodotrema lethrini* Yamaguti, 1938.

Of the 15 species which have been included in *Steringotrema*, we herein consider that only six are valid. They are:

(1) *Steringotrema corpulentum* (Linton, 1905) Manter, 1931; this species occurs off the south-eastern coast of the USA and in the Gulf of Mexico. It has been described by Linton (1905) and figured and commented upon by both Manter (1931) and Sogandares-Bernal & Hutton (1959). It is atypical of the genus in that it possesses a median genital pore and vitelline fields which are confluent dorsally.

(2) *Steringotrema divergens* (Rudolphi, 1809) Odhner, 1911; see p. 239.

(3) *Steringotrema ovacutum* (Lebour, 1908) Yamaguti, 1953; see p. 242.

(4) *Steringotrema pagelli* (van Beneden, 1871) Odhner, 1911; see p. 234.

(5) *Steringotrema phrissovum* (Aldrich, 1961) n. comb.; from the intestine of *Parophrys vetulus* off Washington State, USA. It was originally placed in *Fellodistomum;* but the uterus has several loops in the post-testicular region, the excretory vesicle is 'V'-shaped and the eggs are 'spiny', i.e. ornamented. In addition, the ovary is lobate (the figure suggests that it might be trilobed) and the worm bears a considerable resemblance to *S. ovacutum* from which it differs in egg-size.

(6) *Steringotrema rotundum* Manter, 1954; from the gall-bladder and stomach of *Parapercis colias* off New Zealand. It differs from the other species of the genus in having the vitellarium confined to the region posterior to the middle of the ventral sucker. Yamaguti (1971) considered it to be a *Fellodistomum*; but Armstrong (1974) reinstated it in *Steringotrema* and, with post-testicular uterine coils and a 'V'-shaped excretory vesicle, it would appear to fit comfortably into the latter genus.

The other species which have been included in *Steringotrema* are:

(1) *Steringotrema blennii* (Müller, 1776) Dollfus, 1968; Dollfus (1968) considered this to be the oldest available name for *S. divergens*. Müller's description and figures (Müller, 1776 : 224; 1777 : pl. 30, fig. 5; 1780 : pl. 78, figs 9–12; and 1784 : 116 – see Anker, 1950) show clearly that it is not the same species as *S. divergens* of Rudolphi (1809) as seen and redescribed by Odhner (1911*a*) . In our opinion *Fasciola blennii* of Müller is unrecognizable.

(2) *Steringotrema cluthense* (Nicoll, 1909) Odhner, 1911; original type-species of the genus, herein considered to be a synonym of *S pagelli* (see p. 238).

(3) *Steringotrema crassum* (Manter, 1934) Yamaguti, 1953; this species, originally considered as the type-species of the genus *Megenteron* Manter, 1934, differs from *Steringotrema* in possessing long, wide caeca reaching to the posterior extremity of the long hindbody, a small ventral sucker and a multilobate ovary.

(4) *Steringotrema nakazawai* Kobayashi, 1920; this species occurs in sparid fishes in Japanese waters and has been described by Kobayashi (1920) and Yamaguti (1934: 1938). It is superficially similar to *S. pagelli* (particularly the 'small egg' form), although its sucker-ratio is at the extreme end of the range of this species (Kobayashi's measurements suggests an oral to ventral sucker-ratio of 1 : 5–10, but his figure indicates a ratio of 1 : 3·5. Yamaguti's measurements give ratios of 1 : 4 in 1934 and 1 : 5·2 in 1938). The lobed ovary is said to lie posteromedially to the right testis, an unusual position in this subfamily, and the vitellarium is broken up into 5 or 6 bunches of follicles on each side of the body (Kobayashi, 1920; Yamaguti, 1938). Skrjabin & Koval (1957) use this species as the type of a new genus *Markevitschiella*, and created a new subfamily, the Markevitschiellinae, which differs from the Fellodistominae in the following: 'ventral sucker four to five times larger than oral sucker; loops of uterus in one side of body' (Skrjabin *et al.*, 1964). Although Kobayashi's figure does suggest that the uterus is confined to the left side of the body, his description indicates that this feature may not be significantly different from that of species of *Steringotrema* where the uterus fills most of the hindbody and passes anteriorly on the left side of the body toward the genital atrium. Furthermore, Yamaguti (1938) states 'uterus coiled at posterior end of body and on left of the acetabulum'. With regard to the sucker-ratio, we do not consider it alone to be a feature of generic importance. We are, however, reluctant either to accept or to reject *Markevitschiella* on the evidence in the literature. If the position of the ovary and the divided nature of the vitellarium are constant features, then the genus may be valid.

(5) *Steringotrema ovata* Price, 1934; possibly a species of *Bacciger* (see p. 249).

(6) *Steringotrema ponticum* (Pigulewsky, 1938) Yamaguti, 1953; this species was described briefly by Pigulewsky (1938) from *Engraulis encrasicolus* in the Black Sea as the type-species of the new genus *Ovotrema*. It is possible that this species may be a *Steringotrema*, but the ovary is described as medial and slightly post-testicular. Skrjabin & Koval (1957) and other Soviet workers have considered it a synonym of *Bacciger bacciger* (Rudolphi, 1819) and Yamaguti in a recent work (1971) has followed this; but Margolis & Ching (1965) have argued against this synonymy. It is clear that due to an initial inadequate description the status of this species must remain unresolved; but, at least for the present, we prefer to accept it as a questionable synonym of *B. bacciger* (see p. 254 and p. 259).

(7) *Steringotrema pulchrum* Johnston, 1913; this species was considered to belong to the genus *Lintonium* Stunkard & Nigrelli, 1930, by Skrjabin & Koval (1957), as a synonym of what is now *L. consors* (Lühe, 1906) by Odhner (1928) and as a distinct species of the latter genus by Manter & Pritchard (1962).

(8) *Steringotrema quadrilobatum* (Bazikalova, 1932) Yamaguti, 1958; see above under *Rhodotrema* (p. 232).

(9) *Steringotrema quinquelobatum* (Layman, 1930) Yamaguti, 1953; see above under *Rhodotrema* (p. 232).

Key to the species of *Steringotrema* recorded from the northeast Atlantic

1 Vitellarium divided into 4 zones; ovary globular . . . **S. divergens** (Rudolphi, 1809) (p. 239)
– Vitellarium divided into 2 lateral zones; ovary trilobed 2
2 Vitellarium reaching back to middle of ventral sucker; egg-shell prominently ornamented . . . . **S. ovacutum** (Lebour, 1908) (p. 242)
– Vitellarium reaching back to level of testes; egg-shell smooth or *very* weakly ornamented . . . . **S. pagelli** (van Beneden, 1871) (p. 234)

Steringotrema pagelli (van Beneden, 1871) Odhner, 1911

Distoma pagelli van Beneden, 1871.
Steringotrema (*Ovotrema*) *pagelli* (van Beneden) Yamaguti, 1953.
Distomum tergestinum Stossich, 1888.
Steringophorus cluthensis Nicholl, 1909.
Leioderma cluthense (Nicoll) Nicoll, 1910.
Steringotrema cluthense (Nicoll) Odhner, 1911.

TYPE-HOST AND LOCALITY. *Pagellus bogaraveo*, Louvain, Belgium.

RECORDS
(i) Material studied
(a) From the NE Atlantic

Mature worms

Limanda limanda [?] Carmarthen Bay, Dyfed, Wales (Sept.–Nov., 1976). Collected H. Al-Abdul-Jabbar. BM(NH) 1977.5.9.1–3.

Microstomus kitt [intestine] Plymouth, Devon, England (May, 1972). BM(NH) 1977.5.10.1.

—— [intestine] Lossiemouth, Grampian Region, Scotland (Oct., 1973). BM(NH) 1977.5.10.2–11.

Spondyliosoma cantharus [intestine] Whitby, North Yorkshire, England. Collected by G. A. Boxshall. BM(NH) 1976.1.7.10.

—— [intestine, pyloric caeca] Southern North Sea (Nov., 1960). BM(NH) 1978.1.18.1–15.

—— ['gut'] Scarborough, North Yorkshire, England (Oct., 1976; Nov., 1977; Nov., 1978). Collected by D. Whittaker. BM(NH) 1979.2.14.12–19.

Immature worms

Limanda limanda [stomach & intestine] Plymouth, Devon, England (May, 1932), (see Baylis & Jones, 1933; Baylis, 1939; as *S. cluthense*), BM(NH) 1932.11.25.9 (see Baylis & Jones, 1933; Baylis, 1939, as *Steringophorus furciger*), BM(NH) 1932.11.25.1–8 [intestine] (March, 1969), BM(NH) 1972.3.27.18; (May, 1972), BM(NH) 1977.5.10.2–14.

Microstomus kitt [stomach & intestine] Plymouth, Devon, England (May, 1932) (see Baylis & Jones, 1933; Baylis, 1939; as *S. cluthense*), BM(NH) 1932.11.25.10–11; [intestine] (May, 1972), BM(NH) 1977.5.10.15–19.

—— [intestine] Tjärnö, Sweden (June, 1971). Material of J. Thulin.

—— [pyloric caeca] Moray Firth, Scotland (58°N, 02°W; depth 90–102 m; July, 1976). BM(NH) 1977.5.10.20.

Pleuronectes platessa [intestine] Tjärnö, Sweden (June, 1971). Material of J. Thulin.

—— [intestine] Kristineberg, Sweden (Dec., 1971). Material of J. Thulin.

—— [intestine] Plymouth, Devon, England (May, 1972). BM(NH) 1977.5.10.21.

(b) From elsewhere
None

(ii) NE Atlantic records from the literature

Limanda limanda [stomach & intestine] Plymouth, Devon, England (May, 1932). Baylis & Jones (1933 : 630; as *S. cluthense* and *Steringophorus furciger*); Baylis (1939 : 482; as *S. cluthense* and *Steringophorus furciger*).

Microstomus kitt [duodenum & pyloric caeca] Firth of Clyde, Scotland, Nicoll (1909*a* : 472; as *Steringophorus cluthense*; 1910 : 347; as *Leioderma cluthense*).

—— [intestine] Plymouth, Devon, England. Nicoll (1914 : 478, 502; as *S. cluthense*); [stomach & intestine] (May, 1932) Baylis & Jones (1933 : 630; as *S. cluthense*); Baylis (1939 : 482; as *S. cluthense*).

—— [intestine] Galway, Ireland. Little (1929 : 26, 27; as *S. cluthense*).

Pagellus bogaraveo [stomach] Louvain, Belgium. van Beneden (1871 : 43; as *Distoma pagelli*).

—— [intestine] Billingsgate Fish Market, London (material either from North Sea or from English Channel). Nicoll (1914 : 480).

—— [intestine] Plymouth, Devon, England. Nicoll (1914 : 497).
—— [intestine] Galway, Ireland. Little (1929 : 26, 27).
Spondyliosoma cantharus [pyloric caeca & intestine] Ostende, Belgium. van Beneden (1871 : 43; as *Distoma pagelli*).

Aspects of biology. This species infests, in its adult form, two or three species of flatfish and members of the family Sparidae. It is not known what causes this unusual spread of hosts. All the adult worms we have examined have been found late in the year (September–November), with the exception of one early mature specimen collected at Plymouth in May. In addition to its being found in the northeastern Atlantic as far north as Sweden, this species has also been recorded in the Mediterranean and once (Ronald, 1960) from the Gulf of St Lawrence.

It is apparent that sperm-transfer involves the use of spermatophores (Fig. 9c).

Previous descriptions. van Beneden (1871 : figure only; as *Distoma pagelli*); Stossich (1888 : 102; 1889 : 28; as *Distoma tergestinum*); Nicoll (1909*a* : 472; as *Steringophorus cluthense*); Odhner (1911*a* : 102); Nicoll (1914 : 480); Lopez-Roman & Guevara-Pozo (1974 : 1).

Description. (Figs 9 & 10). Forty-seven whole-mounted mature worms (seven of which were flattened) and 52 whole-mounted immature worms were studied along with six sets of serial sections. These worms are small with a broad pyriform body, the anterior region of which tapers towards a pointed pre-oral lobe under certain fixation conditions (Fig. 9b). The posterior end is rounded, although occasionally bearing a small terminal boss (Figs 9a, b & 10a, b). The dimensions of the worms are given in Table 7. The body surface is smooth. The subglobular *oral sucker* opens subterminally and is much smaller than the large, muscular *ventral sucker*, which is slightly wider than long and lies, deeply embedded, more or less in the middle of the body. In immature worms the sucker-ratio shows a continuous gradation down to a minimum of 1 : 1·3, but in adult worms the sucker-ratio is usually greater than 1 : 2. There is a short prepharynx leading to a subglobular *pharynx*. The oesophagus is distinct and its length is quite variable. It divides at about the middle of the forebody. The caeca reach into the hindbody, passing dorso-laterally

Table 7 Dimensions of *Steringotrema pagelli* from the present material

Hosts	*Limanda limanda*	*Microstomus kitt**	*Microstomus kitt*	*Spondyliosoma cantharus*	*Spondyliosoma cantharus*
Locality	Wales	Plymouth	Lossiemouth	Whitby	North Sea
Length (mm)	1·20–1·85	1·16	1·00–1·15	0·85–1·3	1·08–2·3
Breadth (mm)	0·8–1·0	0·62	0·53–0·62	0·76–1·16	0·64–1·42
Length : forebody ratio	1 : 0·20–0·42	1 : 0·25	1 : 0·31–0·36	1 : 0·20–0·27	1 : 0·25–0·42
Oral sucker (mm)	0·19–0·24 × 0·19–0·21	0·16 × 0·10	0·14–0·10 × 0·13	0·14–0·16 × 0·16–0·23	0·17–0·30 × 0·19–0·33
Ventral sucker (mm)	0·49–0·60 × 0·56–0·66	0·38 × 0·46	0·33–0·36 × 0·36–0·40	0·39–0·64 × 0·52–0·87	0·43–0·80 × 0·46–1·34
Sucker-ratio	1 : 2·9–3·1	1 : 4·6	1 : 3·1–4·5	1 : 3·2–3·8	1 : 2·4–4·2
Pharynx (mm)	0·14 × 0·11–0·12	0·10 × 0·08	0·10 × 0·10	0·07 × 0·10	0·12–0·16 × 0·11–0·16
Oesophagus (mm)	up to 0·145	0·045	0·042	–	0·05–0·16
Cirrus-sac (mm)	0·25–0·29 × 0·15–0·19	0·22 × 0·11	0·18 × 0·12–0·14	0·28–0·35 × 0·12–0·18	0·28–0·44 × 0·15–0·22
Testes (mm)	about 0·20–0·21 dia.	0·17–0·22 × 0·16	–	–	0·17–0·19 × 0·14–0·19†
Ovary (mm)	about 0·12–0·13 across	0·15 × 0·08	–	–	0·18 × 0·11†
Eggs (μm)	43–49 × 31–32	61 × 36	46–66 × 32–46	44–53 × 30–34	48–59 × 31–39

* Mature specimen only.
† Only visible in small specimens.

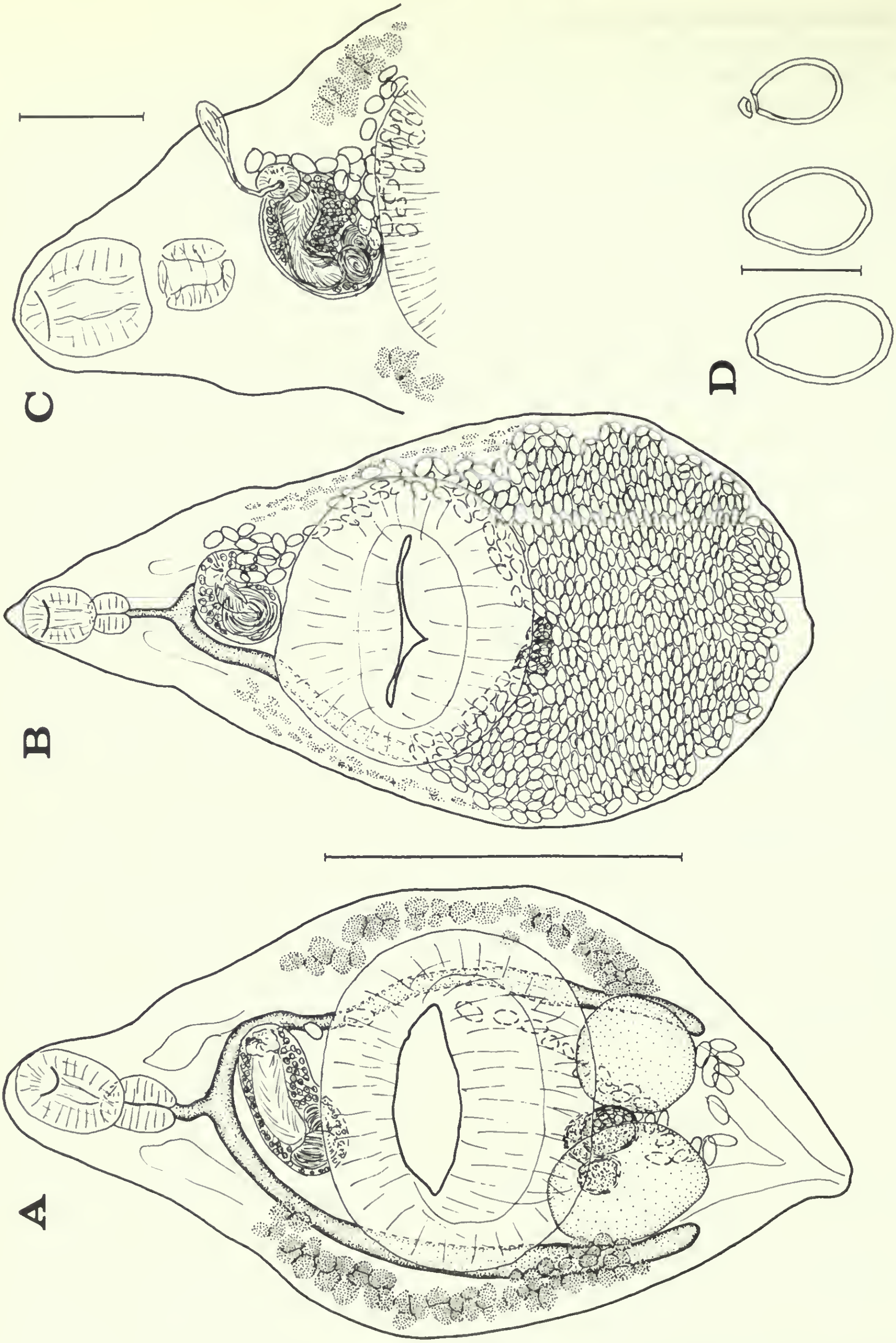


Fig. 9 *Steringotrema pagelli:* (a) young mature specimen from *Microstomus kitt*, Plymouth, May; (b) fully mature specimen from *M. kitt*, Lossiemouth, October; (c) Forebody showing cirrus-sac expelling spermatophore, from *Limanda limanda*, Carmarthen Bay; (d) eggs – left, weakly tanned from *M. kitt*, Plymouth, May; centre, strongly tanned from *M. kitt*, Lossiemouth, October; right, strongly tanned, operculum detached, from *Limanda limanda*. Bar scales: a, b = 0·5 mm; c = 0·2 mm; d = 50 μm.

to the testes, and terminate just at or beyond the posterior margin of the testes, often after having curved ventrally to a position close to the ventral surface of the hindbody.

The *excretory pore* leads into a small spherical chamber from which arise the wide arms of the excretory vesicle. These pass into the forebody, dorsally to the caeca and terminate at the level of the pharynx. Thus the overall pattern is more or less 'V'-shaped.

The *testes* are globular to oval and lie almost symmetrically close to or overlapping the posterior margin of the ventral sucker in the ventral plane. The vasa efferentia pass through the wall of the cirrus sac separately but close together. The *cirrus-sac* is oval and lies close to the anterior margin of the sucker. It contains a bipartite seminal vesicle, a wide, curved pars prostatica and a wide, diverticulate ejaculatory duct (Fig. 10c). The ejaculatory duct may form a cirrus which protrudes through the genital atrium and apparently ejects spermatophores (Fig. 9c). The genital atrium is large, and diverticulate like the ejaculatory duct. Just within the posterior half of the forebody the genital pore opens about midway between the media line and the left margin of the body.

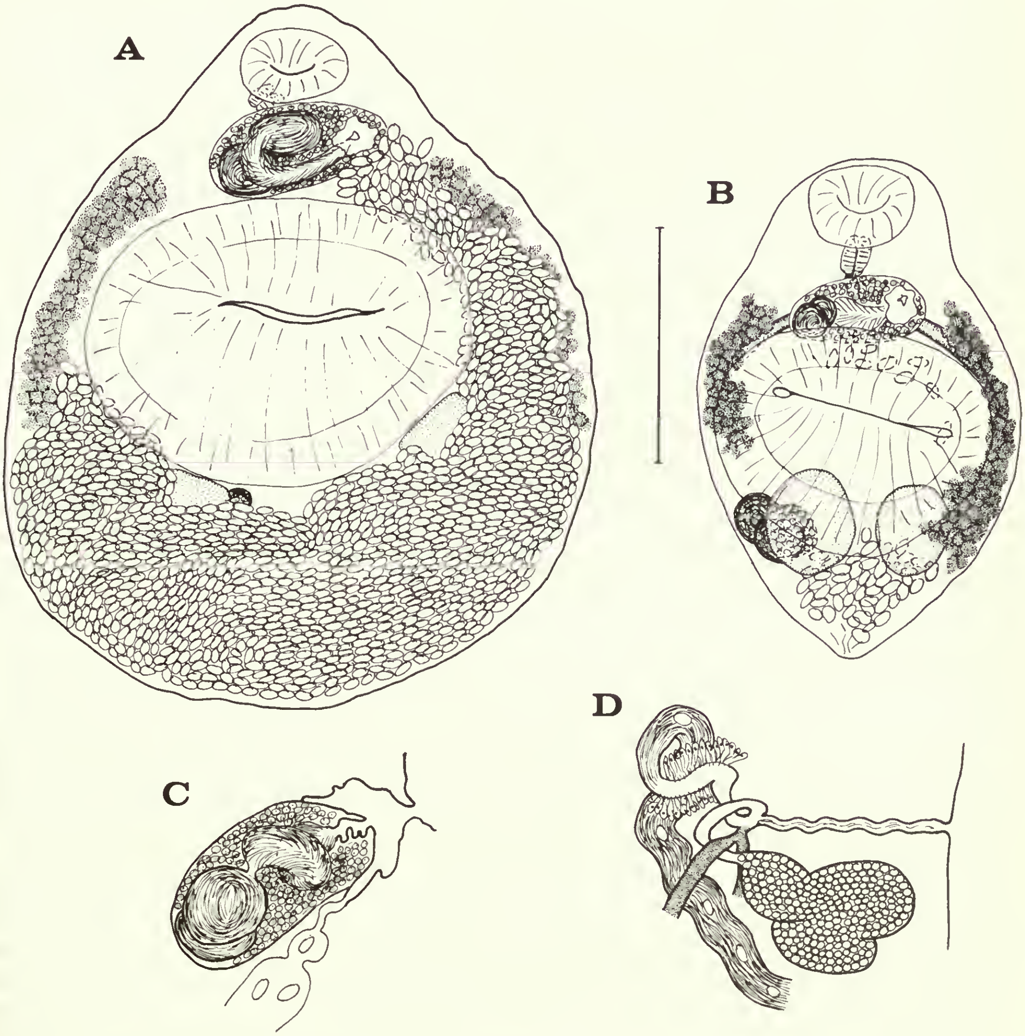


Fig. 10 *Steringotrema pagelli:* (a) flattened specimen from *Spondyliosoma cantharus*, Whitby; (b) young mature specimen, fixed *in situ*, from *S. cantharus*, southern North Sea; (c) cirrus-sac; (d) diagram of female proximal genitalia. Bar scale: a, b = 0·5 mm.

The *ovary* is divided into three irregular lobes and lies dorso-medially or dorso-laterally to the right testis. The oviduct passes ventrally and loops dorsally to a point where it receives Laurer's canal and, apparently, a short common vitelline duct. Laurer's canal is long and wide, containing evidence of spent spermatozoa and ova, and opens dorsally at the level of the ovary (Fig. 10d). Mehlis' gland lies ventrally to the ovary and from it the initial coil of the uterus passes anteriorly and then dorsally and posteriorly to almost envelope the ovarian complex in wide coils packed with spermatozoa. The *uterus* almost completely fills the hindbody in mature specimens, usually obscuring the gonads, and reaching to the posterior extremity. At the level of the ventral sucker it runs forward on the left side of the body and opens into the left side of the genital atrium through a weakly muscular metraterm. In newly mature worms the uterus is initially a single loop which extends into the post-testicular region (Fig. 9a), but in later maturity the uterus occupies much of the hindbody. The numerous eggs are variable in size, being weakly tanned and large in the single mature specimen collected early in the year at Plymouth; but in older worms eggs from the distal region of the uterus are deeply tanned and small, although those in the proximal uterus are weakly tanned and larger. Allowance must be made, therefore, when considering egg measurements, for the state of maturity and the region of the uterus from which the eggs are taken. The eggs, which tend to taper towards the opercular pole (Fig. 9d), have shells which are thick and usually appear smooth, but under very high power optical microscopy some may be seen to be very weakly ornamented. The *vitellarium* consists of two narrow lateral bands of numerous, tightly-packed follicles extending into the forebody to about the level of the genital pore. The posterior limit is often obscured by eggs, but where it can be seen it normally reaches a level between the posterior margin of the ventral sucker and the posterior margin of the testes. Sometimes the posterior termination of the vitellarium is asymmetrical, with one side terminating much further forward than the other (Fig. 10b).

DISCUSSION. The information currently available concerning this species suggests that there are two forms with distinctly different egg-sizes. van Beneden (1871) figured, but did not describe, his material, so the only useful quantitative information which his work provides are the ratios. The egg-measurements were first given by Nicoll (1909*a*) as 44–56 × 28–32 µm from *Microstomus kitt* in the Firth of Clyde, and Odhner (1911*a*) as 48–51 × 28 µm, the hosts being *Cantharus lineatus* and *C. orbicularis* (both now considered synonyms of *Spondyliosoma cantharus*) from Trieste. Shortly afterwards Nicoll (1914) redescribed the species from *Sparus centrodontus* (now *Pagellus bogaraveo*) with eggs of 57–63 × 33–37 µm. His material was collected from Billingsgate Fish Market in London and he was unable to ascertain whether the fish were caught in the North Sea or the English Channel. On page 497 of his paper, however, he lists this host and parasite as having been collected by him at Plymouth. The most recent description of this species is by Lopez-Roman & Guevara-Pozo (1974) from *Spondyliosoma cantharus* in the Mediterranean Sea off Granada, Spain. They quote the egg-size as being 58–60 × 34–36 µm. Our own specimens have eggs ranging from 43–66 × 30–49 µm. A similar variation in egg-size is found in a number of fellodistomines, such as *Steringophorus furciger*, so it would appear that this feature must be treated with a certain amount of caution. As the organs in the hindbody are obscured in fully developed specimens, there must be an inclination towards describing, and thus measuring, the eggs of younger specimens with few eggs in the uterus (see fig. 1 of Lopez-Roman & Guevara Pozo, 1974). In our material the eggs in young worms are larger and less well tanned than those from the distal region of the uterus in fully developed specimens.

Nicoll's (1909*a*) description of *S. cluthense* is the sole source of information on the morphology of that species, and our observations differ from his to some extent. He considered, however, that none of his material was fully mature, and this may account for some of the discrepancies. The sucker-ratio, which he quotes as 1 : 2, varies in our material from the same host between 1 : 1·3 and 1 : 4·6 with the mature specimens having a ratio of 1 : >2·9. There is, therefore, obviously an allometric relationship, with the ventral sucker growing at a much faster rate than the oral sucker. The ovary was described by Nicoll as being small and multilobate; but in our material the immature specimens possess a small ovary with an indistinct irregular outline and in mature specimens this develops into a distinctly trilobed structure.

Nicoll (1909*a*) distinguished *S. cluthense* from *S. pagelli* on the sucker-ratio, the shape of the ovary, the vitelline distribution and the position of the genital atrium. Having studied specimens from both *Microstomus kitt*, the type-host of *S. cluthense*, and *Spondyliosoma cantharus*, one of the original hosts of *S. pagelli*, we have not found that any of these distinctions stand up to critical examination, as can be seen from the above description, Table 7 and Figures 9 and 10. We, therefore, consider *S. cluthense* a synonym of *S. pagelli* despite the rather different hosts usually recorded for these species.

Distoma tergestinum Stossich, 1888, from the sparid *Oblada melanura* in the Adriatic Sea off Trieste was considered a synonym of *S. pagelli* by Odhner (1911*a*), and this is accepted here. Odhner, tentatively, and Dawes (1947) also considered *Distoma actaeonis* Pagenstecher, 1862, from the sea-slug *Elysia viridis* a synonym of *S. pagelli*; but, as the description is meagre and the observation has not been repeated, we have not included it in our list of synonyms.

Steringotrema divergens (Rudolphi, 1809) Odhner, 1911

Distoma divergens Rudolphi, 1809.
Fasciola divergens (Rudolphi) de Blainville, 1820.

TYPE-HOST AND LOCALITY. *Zoarces viviparus*, Rimini, Italy.

RECORDS
(i) Material studied
(a) From the NE Atlantic
Blennius ocellaris [stomach & intestine] Plymouth, Devon, England (May, 1932) (see Baylis & Jones, 1933; Baylis, 1939), BM(NH) 1932.11.25.13–52; material collected in 1932 by J. S. Stewart, BM(NH) 1938.11.4.216–225.
Capros aper [intestine] Bay of Biscay (Jan. 1971) (see Bray, 1973). BM(NH) 1973.5.17.57–59.

(b) From elsewhere
Capros aper [intestine] Atlantic coast of Morocco (see Bray, 1973). BM(NH) 1973.5.17.57–59.

(ii) NE Atlantic records from the literature
Blennius ocellaris [stomach & intestine] Plymouth, Devon, England (June, 1910), Nicoll (1914 : 480, 499); (May, 1932) Baylis & Jones (1933 : 630), Baylis (1939 : 482).
Capros aper [intestine] Bay of Biscay (44°N, 07°W; depth 272–280 m; Jan., 1971). Bray (1973 : 173).
Ciliata mustela [intestine] Lawrenny, Dyfed, Wales (Sept., 1964). Crothers (1966 : 23).

ASPECTS OF BIOLOGY. Palombi (1931*b*) described and figured a pair of *S. divergens* in a 'pre-copulazione' condition. He also showed a 'cordono fibroso' reaching between the lumina of the ventral suckers. This may be a spermatophore, but the description is not detailed enough for us to be certain. Palombi apparently believed that copulation occurred in this species with Laurer's canal functioning as a vagina; but evidence from other fellodistomines, e.g. *Fellodistomum fellis* (see p. 206), and the presence of a uterine seminal receptacle suggests that this is extremely unlikely.

The southern region of the British Isles appears to be the northern limit of the distribution of this species, which also occurs in the Bay of Biscay, the Mediterranean Sea and the western coast of Africa as far south as Morocco and possibly Senegal. Its usual hosts are blennies and eelpouts, but recently it has been found in fishes from deeper waters, such as *Capros aper* (Bray, 1973) and a questionable record in *Pagellus bogaraveo* [the type-host of *S. pagelli*] (Fischthal & Thomas, 1972*b*).

PREVIOUS DESCRIPTIONS. Odhner (1911*a* : 103); Nicoll (1914 : 480; brief comments); Palombi (1931*a* : 1); Mathias (1934 : 567); Bray (1973 : 173); Lopez-Roman & Guevara-Pozo (1974 : 4).

DESCRIPTION (Fig. 11). This description is based upon 44 whole-mounted and three sectioned

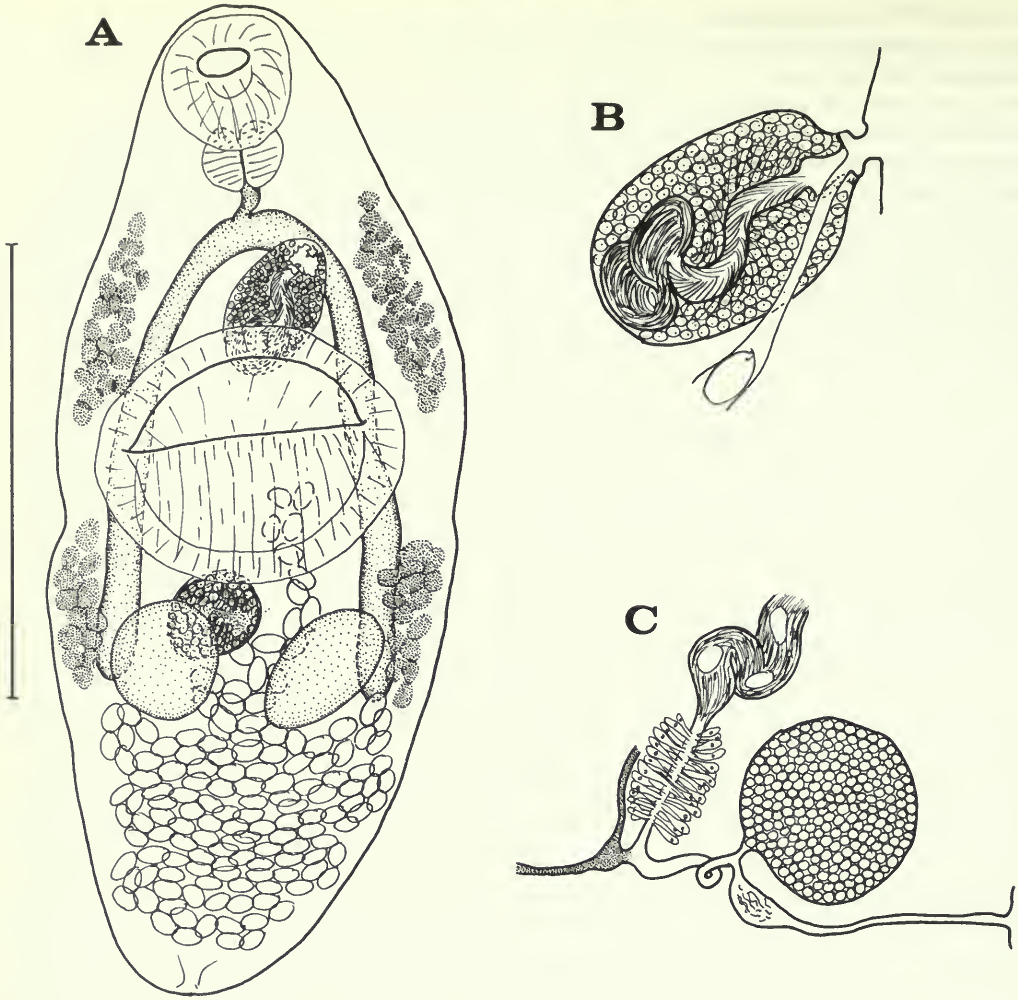


Fig. 11 *Steringotrema divergens:* (a) whole-mount specimen from *Blennius ocellaris*; (b) cirrus-sac; (c) diagram of female proximal genitalia. Bar scale: a = 0.5 mm.

specimens. The worm is of an elongate oval shape, sometimes showing a slight 'waist' at the level of the ventral sucker (Fig. 11a). The tegument is unarmed. The dimensions of this worm are given in Table 8. The globular, subterminal *oral sucker* is usually at most half the size of the larger, globular *ventral sucker*, which is situated just anterior to the middle of the body. There is a short prepharynx, which leads into a well-developed, globular *pharynx*. The oesophagus is short, bifurcating at about the level of the genital pore and giving rise to the two gut-caeca which reach back to about the level of the posterior margin of the testes.

The terminal *excretory pore* leads into a 'V'-shaped vesicle, the arms of which reach forward dorso-laterally to the level of the pharynx.

The oval *testes* lie close to the posterior margin of the ventral sucker in a symmetrical formation. The vasa efferentia pass separately, but close together, through the wall of the cirrus-sac. The *cirrus-sac* is broadly oval and may just overlap the ventral sucker posteriorly (Fig. 11a & b). It contains a bipartite, saccular seminal vesicle, a recurved and narrow pars prostatica with a filamentous lining, and a wide and diverticulate ejaculatory duct. In some specimens the seminal vesicle is empty and forms a simple tube. The genital atrium is quite small and opens ventrally through the genital pore just to the left of the median line in about the middle of the forebody.

The subglobular *ovary* lies anteriorly or antero-medially to the right testis. From its ventral surface the oviduct arises and passes ventrally following a convoluted course. Almost immediately after leaving the ovary it receives Laurer's canal, which may be slightly dilate proximally and contain a few spermatozoa. Laurer's canal opens dorsally at about the level of the posterior margin of the ovary (Fig. 11c). Just prior to entering a weakly developed Mehlis' gland which lies ventrally to the ovary, the oviduct receives the common vitelline duct. The proximal region of the *uterus* forms a uterine seminal receptacle. The majority of the remainder of the uterus, which contains numerous operculate and smooth-shelled eggs, is coiled in the post-testicular region of the hindbody, but a narrow section passes anteriorly between the testes and opens into the genital atrium from the left side via a narrow, muscular metraterm. The follicular *vitellarium* is disposed in four small groups laterally and symmetrically, two in the forebody and two in the anterior hindbody. The fields in the forebody reach from the level of the pharynx or the intestinal bifurcation to the level of the anterior third of the ventral sucker, and the fields in the hindbody extend from the level of the posterior margin of the ventral sucker to about the level of the posterior margin of the testes. The main lateral vitelline ducts unite ventrally to the ovary to form a short common vitelline duct, which is slightly dilate and thus forms a small vitelline reservoir prior to uniting with the oviduct (Fig. 11c).

Table 8 Dimensions of *Steringotrema divergens* from the present material and from the literature

Authority	Mathias (1934)	Bray (1973)	Lopez-Roman & Guevara-Pozo (1974)	Present material
Host	*Blennius ocellaris*	*Capros aper*	*Blennius ocellaris*	*Blennius ocellaris*
Locality	Banyuls	Bay of Biscay & Morocco	Spain	Plymouth
Length (mm)	0·97–2·0	0·75–1·2	1·6–1·75	0·92–1·14
Breadth (mm)	0·5–1·0	0·42–0·47	0·72–0·79	0·44–0·48
Length : forebody ratio	(1 : 0·41)	1 : 0·20–0·42*	(1 : 0·38)	1 : 0·29–0·40
Oral sucker (mm)	0·15–0·20	0·11–0·15 dia.	0·16–0·21 × 0·195–0·26	0·12–0·16 × 0·14–0·16
Ventral sucker (mm)	0·28–0·40 × 0·35–0·48	0·21–0·31 × 0·38–0·42	0·36–0·41 × 0·40–0·45	0·26–0·30 × 0·32–0·38
Sucker ratio	(1 : 2·3)	1 : 2·7–3·6	(1 : 2·2)	1 : 2·0–2·7
Pharynx (mm)	0·10–0·15	0·9–0·11 dia.	0·12–0·14 × 0·15–0·18	0·10–0·12 dia.
Oesophagus (mm)	–	–	–	about 0·12–0·19
Cirrus-sac (mm)	0·20–0·30 × 0·15–0·20	0·18–0·19 × 0·11–0·13	(0·29 × 0·15)	0·19 × 0·13
Testes (mm)	0·13–0·18 × 0·18–0·28	–	0·13–0·195 × 0·12–0·15	0·13–0·17 × 0·11–0·13
Ovary (mm)	0·10–0·17 × 0·10–0·19	–	0·105–0·13 × 0·074	0·08–0·13 × 0·09–0·10
Eggs (μm)	40–55 × 22–32	46–48 × 33–37	47–49 × 30–33	44–55 × 28–36

* New data.

Discussion. The unique vitelline distribution of this worm sets it apart from other species of the genus. Nicoll (1914) described the ovary as being indistinctly trilobate, but most descriptions and our own material indicate that the ovary is normally more or less globular, although it may have slightly indented margins. Palombi (1931*a*) described and figured a seminal receptacle. This appears to be the slightly dilate part of Laurer's canal that we have observed, which may contain small numbers of, presumably, spent spermatozoa. As a uterine seminal receptacle is present, this is unlikely to actually function as a seminal receptacle. It is probably identical to the structure which we have referred to as a 'rudimentary seminal receptacle' in hemiuroids (Gibson & Bray, 1977: 168; 1979: 50).

Steringotrema ovacutum (Lebour, 1908) Yamaguti, 1953

Steringophorus ovacutus Lebour, 1908.
Rhodotrema ovacutum (Lebour) Odhner, 1911.
Stenakron ovacutus (Lebour) Strelkov, 1960.

TYPE-HOST AND LOCALITY. *Hippoglossoides platessoides*, Northumberland coast, England.

RECORDS
(i) Material studied
(a) From NE Atlantic

Mature worms
Hippoglossoides platessoides [intestine] Cullercoats, Northumberland, England (May, 1972). Material of J. Thulin.

Immature worms
Hippoglossoides platessoides [intestine] Aberdeen, Scotland (Oct., 1973) BM(NH) 1977.5.25.7.
Lycodes vahli [intestine] Kristineberg, Sweden (Dec., 1971). Material of J. Thulin.

(b) From elsewhere

Mature worms
Hippoglossoides platessoides [intestine] Newfoundland and Nova Scotia (see Bray, 1979 : 420). BM(NH) 1977.2.16.57–64.

Immature worms
Anarhichas lupus [intestine] Newfoundland (see Bray, 1979 : 420). BM(NH) 1977.2.16.56.
Hippoglossoides platessoides [intestine] Newfoundland and Labrador (see Bray, 1979 : 420). BM(NH) 1977.2.16.57–64.
Lycodes vahli [intestine] Newfoundland (see Bray, 1979 : 420). BM(NH) 1977.2.16.65.

(ii) NE Atlantic records from the literature
Hippoglossoides platessoides [intestine] Northumberland coast, England (June, Nov., 1907). Lebour (1908*a* : 35; 1908*b* : 42; as *Steringophorus ovacutus*).
—— [intestine] Kristineberg, Sweden. Odhner (1911*a* : 100; as *Rhodotrema ovacutum*).
– [intestine] Aberdeen, Scotland. Nicoll (1913 : 190; as *Rhodotrema ovacutum*).

ASPECTS OF BIOLOGY. The life-history of this parasite is not known, although Scott (1975*a*), after having noted that the incidence of the worm in *Hippoglossoides platessoides* of various sizes paralleled that of the incidence of sea-urchins and sand-dollars in their food, suggested that these particular animals 'merited investigation as potential intermediate hosts'.

All of our adult worms came from the long-rough dab (*H. platessoides*), and prior to this work it was the only known host in the NE Atlantic region. It appears, however, that the worm can survive for a time, although apparently not mature, in the blennioid fishes *Lycodes vahli* and *Anarhichas lupus*. The distribution of *S. ovacutum* extends from the eastern coast of Canada across the northern North Atlantic to the Barents Sea, the Mediterranean Sea and in the northern North Pacific from the Bering Sea through the Sea of Okhotsk to the Sea of Japan. Throughout its distribution this species appears to have a definite predilection for pleuronectid hosts.

PREVIOUS DESCRIPTIONS. Lebour (1908*b* : 42; as *Steringophorus ovacutus*); Odhner (1911*a* : 100; as *Rhodotrema ovacutum*); Polyansky (1955 : 54; as *Rhodotrema ovacutum*); Skrjabin & Koval

(1957 : 250; as *Rhodotrema ovacutum*); Zhukov (1960 : 32; as *Rhodotrema ovacutum*); Mamaev *et al*. (1963 : 96; as *Rhodotrema ovacutum*).

Description (Fig. 12). Only six mature specimens were available for study, one of which was serially sectioned, and numerous immature specimens, one of which was also sectioned. The dimensions of this species are summarized in Table 9. This worm is ovoid (Fig. 12a & b) and the body-surface is smooth. There is a subterminal, globular *oral sucker*, which is normally slightly more than half the breadth of the bulky, muscular *ventral sucker*. The latter sucker is situated in the middle (in immature worms) or slightly anterior to the middle (in mature worms) of the body and possesses an aperture which is often directed anteriorly. There is a short prepharynx that leads into a well-developed globular *pharynx*. The oesophagus is also short and is surrounded by gland-cells. The intestinal bifurcation occurs between the middle of the forebody and the anterior margin of the ventral sucker (Fig. 12a & b). The usually wide caeca reach back into the hindbody to a position lateral to the testes, where they terminate blindly.

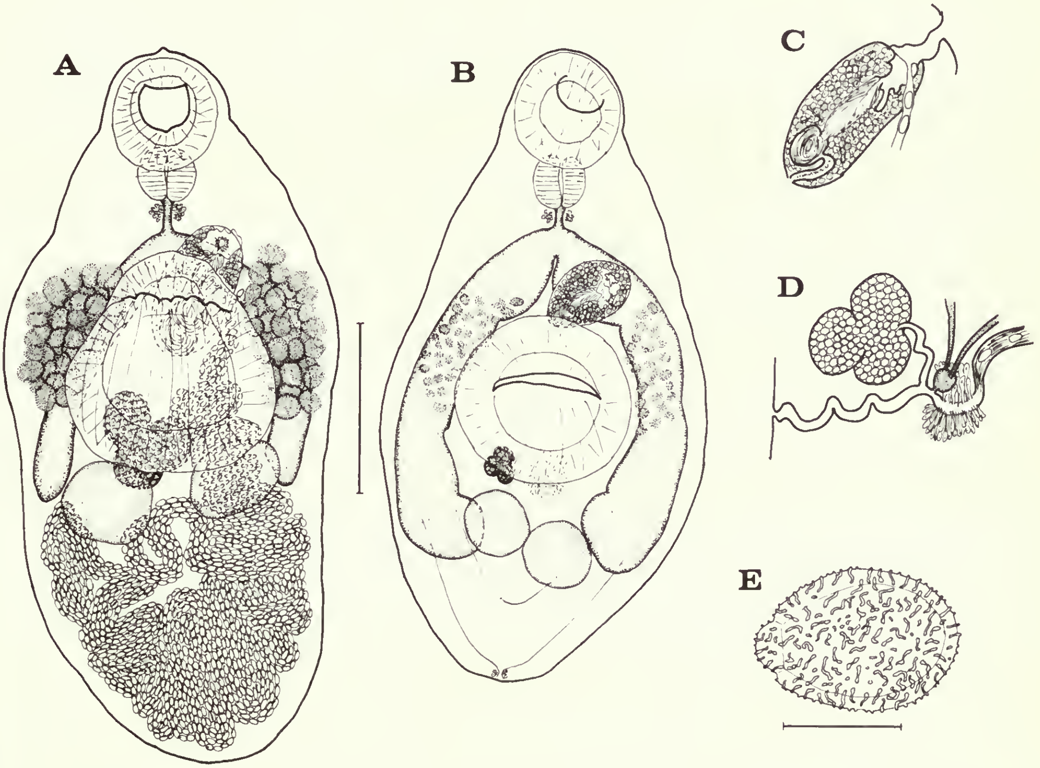


Fig. 12 *Steringotrema ovacutum:* (a) mature specimen from *Hippoglossoides platessoides:* (b) immature specimen from *Anarhichas lupus*; (c) cirrus-sac; (d) diagram of female proximal genitalia; (e) egg. Bar scale: a, b = 0·5 mm; e = 50 μm.

The *excretory pore* is terminal and leads into a 'V'-shaped vesicle with a dilate base and wide arms in the hindbody (Fig. 12b). In the forebody the arms become narrower and reach to the level of the pharynx.

The *testes* are oval to globular and are arranged more or less symmetrically close to the posterior margin of the ventral sucker in the ventral plane: the testes are especially close to the ventral sucker in mature specimens. The vasa efferentia are difficult to follow but appear to pass through the wall of the cirrus-sac close together, but separately. The *cirrus-sac* is an oval structure containing the seminal vesicle, pars prostatica and ejaculatory duct. The seminal vesicle is

Table 9 Dimensions of *Steringotrema ovacutum* from the present material and from the literature

Authority	Lebour (1908*b*)	Odhner (1911*a*)	Zhukov (1960, and in Skrjabin & Koval, 1957)	Present material
Hosts	*Hippoglossoides platessoides*	*Hippoglossoides platessoides*	*Hippoglossoides elassodon dubius*, *Cleisthenes herzensteini*	see text
Locality	Northumberland	W. Sweden	Sea of Japan	see text
Length (mm)	1·8–2·3	1·2–1·5	1·8–3·93	0·81–2·3
Breadth (mm)	1·16–1·33	0·55–0·63	1·31–2·1	0·49–1·08
Length : forebody ratio	(1 : 0·38)	(1 : 0·26)	(1 : 0·36)	1 : 0·29–0·49 (immature) 1 : 0·26–0·36 (mature)
Oral sucker (mm)	0·32–0·40 across	0·25–0·27	–	0·11–0·42 × 0·15–0·39
Ventral sucker (mm)	0·6–0·8 across	0·4–0·5	–	0·30–0·68 × 0·32–0·81
Sucker-ratio	1 : 2	(1 : 1·9)	(1 : 1·8)	1 : 1·6–2·6
Pharynx (mm)	–	0·11–0·13	–	0·10–0·22 × 0·10–0·19
Oesophagus (mm)	–	–	–	0·03–0·1
Cirrus-sac (mm)	0·3 long	–	–	0·10–0·37 × 0·10–0·22
Testes (mm)	0·12 long	–	–	0·06–0·29 × 0·06–0·27
Ovary (mm)	–	–	–	0·11–0·31 × 0·09–0·26
Eggs (μm) *	46 × 26	48 × 28	46–50 × 29–33	38–50 × 29–38

* Further egg measurements: 36–50 × 21–29 (Polyansky, 1955).

bipartite, normally consisting of two globular or short, cylindrical parts which are distended with spermatozoa (Fig. 12a); but in some specimens it may be almost empty and reduced to a narrow tube (Fig. 12c). The wide pars prostatica is almost straight and lined with filamentous projections, and the muscular wall of the ejaculatory duct has many irregular diverticula. The genital atrium is small and opens ventrally through the genital pore, which lies to the left of the median line in the posterior half of the forebody.

The trilobed *ovary* has a clover leaf-like outline, and lies dorsally to the posterior margin of the ventral sucker. It lies in a more dorsal plane than the testes, and is situated anterior or anteromedial to the right testis. The oviduct passes ventrally from the ovary, and prior to entering Mehlis' gland it receives Laurer's canal and the common vitelline duct (Fig. 12d). Laurer's canal opens dorsally at the level of the posterior margin of the ovary, after having followed a convoluted course. A uterine seminal receptacle is present. The bulk of the *uterus* lies posterior to the testes, normally filling the entire post-testicular region of the hindbody in mature specimens. The distal region of the uterus passes anteriorly dorsal to the left side of the ventral sucker, and opens into the genital atrium from the left. The numerous, operculate eggs vary considerably in size and have a distinctive type of pattern etched onto the surface of the shell (Fig. 12e). The *vitellarium* consists of two lateral fields of tightly packed follicles, which are situated symmetrically. These fields extend from a level between the intestinal bifurcation and the anterior margin of the ventral sucker to a posterior limit between the middle and the posterior margin of the ventral sucker. The follicles feed two main lateral ducts which unite to form a short common duct lying adjacent to Mehlis' gland. The common duct is distended to form a small vitelline reservoir (Fig. 12d).

Discussion. This species possesses eggs with ornamented or etched shells. This feature has also been illustrated by Mamaev *et al*. (1963); but it is surprising that it has not been commented on prior to this, especially as some of the earlier workers have obviously examined the eggs carefully. Lebour (1908*b*), for example, coined the specific name because of what she considered to be the unusual shape of the eggs. A similar ornamentation of the egg-shell probably occurs in the similar species *S. phrissovum* (Aldrich, 1961), where the eggs are described as spiny, and also in more distantly related fellodistomines, such as *Benthotrema plenum* Manter, 1934, and *Steringophorus blackeri* Bray, 1973.

This species was used by Odhner (1911*a*) to erect the genus *Rhodotrema*, which is supposed to differ from *Steringotrema* in possessing a 'Y'-shaped excretory vesicle, a shorter and more muscular pars prostatica and a less rounded cirrus-sac. The excretory vesicle is, however, practically 'V'-shaped, and the other two characters, which are open to doubt, are not criteria of importance at the generic level. There appears, therefore, to be no good reason for maintaining *Rhodotrema* as a distinct genus. The confusion between *Rhodotrema* and members of the Stenakrinae Yamaguti, 1970, which has led to a number of species (see p. 232) being erroneously placed in this genus, is probably due to Odhner's (1911*a*) figure, which is of an immature worm and gives no indication of the full uterine distribution. In the Stenakrinae the uterus is confined to the pre-testicular region. Other points of difference between the latter group and the fellodistomines are listed on p. 201.

Genus ***PRUDHOEUS*** gen. nov.

Definition. Body small, elongate oval. Body-surface smooth. Oral sucker globular; subterminal. Ventral sucker transversely oval; much larger than oral sucker; inside anterior half of body. Hindbody longer in mature specimens than in immature worms. Prepharynx small. Pharynx oval, well developed. Oesophagus short. Intestinal bifurcation near middle of forebody; caeca end blindly close to posterior extremity. Testes two; irregularly rounded to oval; more or less symmetrical in anterior hindbody; post-ovarian. Cirrus-sac oval; containing bipartite seminal vesicle, wide pars prostatica with external gland-cells and filamentous lining, and well-developed ejaculatory duct [wide and diverticulate in other members of subfamily]. Well-developed cirrus often present. Genital atrium present; shallow. Genital pore ventrally submedian, sinistral; at about level of intestinal bifurcation; may be wide when cirrus everted. Spermatophores may be present. Ovary trilobed; anterior to right testis or approximately median. Laurer's canal and uterine seminal receptacle present. Uterus mainly post-testicular; reaches to posterior extremity. Eggs small; operculate; without spines, filaments or ornamentation on shell. Vitellarium follicular; in two lateral fields; mainly in ventro-lateral plane; between the level of the posterior margin of ventral sucker and a level posterior to the middle of the hindbody; fields may almost unite ventrally. Excretory pore terminal; vesicle 'V'-shaped, with arms reaching into forebody. Parasitic in upper intestine of marine teleosts.

Type-species. *Prudhoeus nicholsi* sp. nov.

Comment. This new genus is probably most closely related to *Lomasoma* Manter, 1935, and *Lissoloma* Manter, 1934. It differs from the former in lacking any lateral lobation of the body, from the latter in body-shape, and from both in possessing a trilobed, rather than a multilobate, ovary, in lacking polar processes or filaments on the eggs and in having much of the vitellarium in the ventral plane.

This genus is named in honour of our colleague Mr S. Prudhoe OBE for contributions to helminth-taxonomy and the years of advice from which we have benefited.

Prudhoeus nicholsi sp. nov.

Type-host and locality. *Polyacanthonotus rissoanus*, off W of Ireland (55°N, 10°W).

Records
(i) Material studied
(a) From the NE Atlantic

Polyacanthonotus rissoanus [upper intestine] Off St Kilda, Scotland (57°N, 09°W; depth 980–1030 m; June, 1974). BM(NH) (paratype) 1977.6.14.366.

—— [upper intestine] W of Tory Island, off W of Ireland (55°N, 10°W; depth 800–825 m; June, 1974). BM(NH) (holotype) 1977.6.14.365; (paratypes) 1977.6.14.367.

—— [intestine] Flannan region, NW of Scotland (58°N, 10°W; depth 1300–1320 m; Oct., 1978). BM(NH) 1979.2.14.7–11 (paratypes).

ASPECTS OF BIOLOGY. According to Wheeler, in Hureau & Monod (1973), *Polyacanthonotus rissoanus*, the host of this species, is benthic, occurring in deep waters of the Mediterranean and eastern Atlantic off Morocco. Our observations indicate that this fish also occurs on the edge of the continental shelf further to the north. It appears that, like *Steringophorus pritchardae* and *Olssonium turneri*, this species is a deep-water form. It appears that spermatophores are used in sperm-transfer.

PREVIOUS DESCRIPTIONS. None.

DESCRIPTION (Fig. 13). Fifteen worms were found, two of which were serially sectioned. Three of the worms are in an early mature condition (Fig. 13b). The larger adult worms are elongate oval, and it is apparent that the hindbody increases in size relative to the forebody at a much faster rate as the worm grows (cf. Figs 13a & b). The body-surface is smooth, and the sub-tegumentary parenchyma contains many gland-cells. The body-length varies between 1·24 and 2·90 mm and the maximum width between 0·37 and 0·86 mm. The forebody, which tapers sharply, is less than a quarter (0·17–0·22) of the body-length in the largest specimens, but a much greater

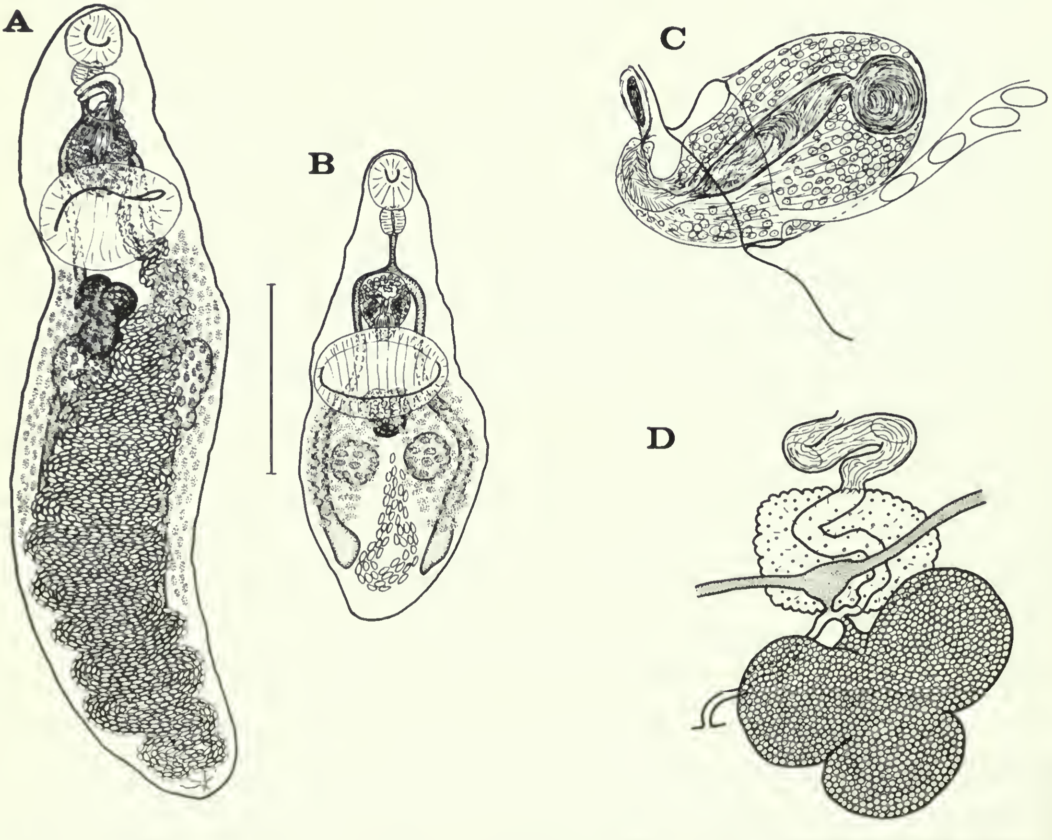


Fig. 13 *Prudhoeus nicholsi:* (a) large specimen, ventral view; (b) small specimen, ventral view; (c) cirrus-sac; (d) diagram of female proximal genitalia. Bar scale: a, b = 0·5 mm.

proportion (0·26–0·37) of the body-length in the smaller specimens. The hindbody, when filled with the voluminous uterus, has roughly parallel sides with a rounded or slightly indented posterior margin, but in the smallest specimen it is broadly oval. The subglobular, subterminal *oral sucker* (0·11–0·20 × 0·10–0·17 mm) is smaller than the transversely oval *ventral sucker* (0·23–0·40 × 0·26–0·43), the ratio being 1 : 2·3–3·7. The aperture of the ventral sucker may be directed anteriorly. There is a very short prepharynx, which leads into a globular *pharynx*, measuring about 0·064–0·09 mm in diameter. The short oesophagus (0·05–0·10 mm in length) bifurcates at about the middle of the forebody, and the caeca, which are narrow and straight, reach into the posterior half of the post-testicular zone, where they end blindly.

The *excretory pore* is terminal and leads into a short, narrow glandular duct which leads into a 'V'-shaped vesicle. The arms reach dorso-laterally into the forebody to the level of the cirrus-sac.

The irregularly rounded to oval *testes* (0·16–0·29 × 0·08–0·19 mm) lie symmetrically or slightly obliquely in the anterior hindbody. The vasa efferentia pass close together, but separately through the wall of the cirrus-sac. The *cirrus-sac* (0·16–0·24 × 0·12–0·20 mm) lies in the posterior forebody, slightly overlapping dorsally the anterior margin of the ventral sucker. It is globular to oval, and contains a bipartite seminal vesicle, a wide pars prostatica with external gland-cells and filamentous lining and an ejaculatory duct. The proximal region of the seminal vesicle is globular and the distal region is oval. In two of our specimens, including the sectioned specimen, the cirrus is everted, thus modifying the normal arrangement of the contents of the cirrus-sac. The pars prostatica is typical of the subfamily, but in the everted specimens it is pushed forward into the cirrus (Fig. 13c): this movement may also be partly responsible for the elongate oval shape of the distal part of the seminal vesicle. The ejaculatory duct of the everted specimens forms the outer wall of the cirrus. When the cirrus is withdrawn the ejaculatory duct is wide and diverticulate, as it is in other fellodistomines. When everted the cirrus is a large conical structure which extends through the genital pore. In the sectioned specimen a spermatophore can be seen lying close to the end of the cirrus. The genital atrium appears to be shallow, although like the genital pore, which is situated just to the left of the median line at about the level of the intestinal bifurcation, it appears to be wide when the cirrus is everted.

The trilobed *ovary* (0·16–0·26 × 0·13–0·24 mm) lies antero-medially to the right testis, or in the median line, close to the posterior margin of the ventral sucker. The short oviduct passes anteroventrally from the ovary to Mehlis' gland. Prior to its entry into Mehlis' gland it receives Laurer's canal and the common vitelline duct (Fig. 13d). Laurer's canal passes over the posterior surface of the ovary and opens dorsally at the level of the testes. A uterine seminal receptacle is present, formed by the initial loops of the *uterus*, the majority of which is coiled in the post-testicular zone. The loops of the uterus extend from the posterior end of the body forward through the intertesticular region to the level of the ovary and a single uterine sling reaches anteriorly towards the genital atrium into which it opens to the left of the cirrus-sac. The numerous, operculate eggs (36–44 × 21–25 µm) lack spines, filaments or ornamentation on the shells. The *vitellarium* is follicular, lying in two lateral fields reaching from the level of the posterior margin of the ventral sucker to just inside the posterior half of the hindbody. The follicles lie mainly in the ventral parenchyma, but pass laterally to the caeca and just into the dorsal field. In the anterior region of the hindbody the vitelline fields come close together ventrally as they are wider in this region. The main lateral vitelline ducts unite ventrally to Mehlis' gland to form the common vitelline duct, which is enlarged proximally to form a distinct vitelline reservoir.

DISCUSSION. Probably the most similar species to *P. nicholsi* in our region is *Steringophorus furciger*. The two can, however, easily be distinguished by the shape of the excretory vesicle, the shape of the ovary, the length of the caeca and the distribution of the vitellarium. This species is also similar to *Steringotrema* sp. of Armstrong (1974) from the macrourid *Ventrifossa atlantica* in the eastern Gulf of Mexico. The sucker-ratio of this unnamed species is smaller ['1 : 1·8–2·2 (2·8 in one specimen)']. The supposed claviform nature of the seminal vesicle and the absence of Laurer's canal also serve to differentiate it from *P. nicholsi*.

This species is named in honour of Mr John H. Nichols of the MAFF Laboratory, Lowestoft, for his help to one of us (R. A. B.) on numerous occasions.

Subfamily **BACCIGERINAE** Yamaguti, 1958

Pentagramminae Yamaguti, 1958.

DIAGNOSTIC FEATURES. Body small; oval to fusiform. Body-surface smooth or finely spined. Oral sucker subterminal; smaller to larger than ventral sucker. Ventral sucker in middle or anterior half of body. Prepharynx short. Pharynx small; globular to oval. Oesophagus distinct; short to long. Intestinal bifurcation in forebody. Caeca reaching to testicular region or just beyond. Testes two; symmetrical to slightly oblique; in anterior hindbody. Cirrus-sac thin-walled or occasionally absent. Seminal vesicle bipartite; large; enclosed in cirrus sac when latter present. Pars prostatica apparently absent or short; tubular with few external gland-cells. Ejaculatory duct short, narrow; may evert to form small cirrus. Genital atrium deep, narrow. Genital pore median or submedian in posterior forebody. Ovary oval to lobed; inter- or post-testicular. Laurer's canal present; long, opening at or near posterior extremity; proximal region dilated to form canalicular seminal receptacle. Uterine seminal receptacle absent. Uterus almost entirely post-testicular; extensive; opens into genital atrium at base of cirrus-sac. Eggs numerous; small; operculate; shells smooth, without spines or filaments. Vitellarium in two fields, each with one or several compact clusters of small follicles; fields symmetrical in lateral regions of forebody or anterior hindbody; vitelline ducts wide, conspicuous. Excretory vesicle 'Y'-shaped, with short stem (in fact almost 'V'-shaped); arms reach into forebody. Parasitic in intestine and stomach of marine and brackish water teleosts.

COMMENT. Yamaguti (1958) erected the Baccigerinae for *Bacciger* Nicoll, 1914, as a subfamily of the Cryptogonimidae Ward, 1917, and the Pentagramminae for *Pentagramma* Chulkova, 1939, as a subfamily of the Fellodistomidae. He later (1971) considered the Baccigerinae to be a fellodistomid subfamily, containing *Bacciger*, *Faustula* Poche, 1926, *Pseudobacciger* Nahhas & Cable, 1964, and *Pseudopentagramma* Yamaguti, 1971 (a replacement name for the pre-occupied *Pentagramma*). We agree with his later work, as far as the genera *Bacciger* and *Pseudopentagramma* (which we call *Pronopryma* – see below) are concerned, considering them to be morphologically similar enough to be placed in the same subfamily. The structure of the contents of the cirrus-sac and the proximal part of the female reproductive system are especially similar in these two genera. They have not generally been considered to be closely related, however, although *Bacciger* was originally placed in the Fellodistomidae and *Pentagramma* in the Steringophoridae. Yamaguti (1938, 1953) considered *Bacciger* to be a heterophyid, and, as mentioned above, in 1958 he considered it a cryptogonimid. Baer & Joyeux (1961) listed *Bacciger* as a cryptogonimine and *Pentagramma* as a fellodistomine. A detailed taxonomic history of the two genera was presented by Margolis & Ching (1965), and they pointed out that, despite Yamaguti's views at that time, Manter (1947) had retained *Bacciger* in the Fellodistomidae on the basis of the presence of a cirrus-sac. Mehra (1963) also considered *Bacciger* a fellodistomid, pointing out that its life-history is most dissimilar to that of the cryptogonimids. With regard to the Pentagramminae Mehra (1963) considered it synonymous with the Antorchiinae Yamaguti, 1958 [*sic*]. The Antorchiinae Skrjabin & Koval, 1957 (syn. Parantorchiinae Yamaguti, 1958 – see Machida, 1975) certainly contains species similar to those of the Baccigerinae, suggesting strongly that the relationship between these subfamilies is worth further study. A few differences are, however, apparent: these include the nature of the contents of the cirrus-sac and both the presence of dorsal pouches and the presence of the gonads in the forebody in the Antorchiinae. In the present work *Faustula* (syn. *Orientophorus* Srivastava, 1935) is not considered to be a member of the Baccigerinae, as it apparently differs in the shape of the seminal vesicle, the nature of the vitellarium and the presence of a deeply multilobate ovary. If further study indicates that a wider concept of the Baccigerinae including the Antorchiinae is appropriate, then *Faustula* would comfortably fit into such a concept.

The Baccigerinae is probably one of the most aberrant of the fellodistomid groups, having a canalicular seminal receptacle, a long, narrow genital atrium and often fine spines on the body-surface. In addition, it sometimes lacks a cirrus-sac. The spines, when present, are apparently easily lost or not seen, and are probably not similar in construction to those of such prominently spined groups as the zoogonids or lepocreadiids. They are too small to be studied satisfactorily by light microscopy, but, as yet, no studies have been carried out on the species of this group using more critical techniques.

Key to the genera of the Baccigerinae recorded from the northeast Atlantic

1 Body-surface covered with minute spines; body oval; cirrus-sac globular; papilla-like cirrus normally present; ovary intertesticular; Laurer's canal opens at posterior extremity; vitellarium 3 to 4 clusters of follicles in each lateral field, normally in forebody ***BACCIGER*** Nicoll, 1914 (p. 249)

– Body-surface smooth; body fusiform; cirrus-sac elongate; cirrus not normally present; ovary post-testicular; Laurer's canal opens on dorsal surface close to posterior extremity; vitellarium one cluster of small follicles in each lateral field, in hindbody ***PRONOPRYMNA*** Poche, 1926 (p. 254)

Genus *BACCIGER* Nicoll, 1914

(?) *Ovotrema* Pigulewsky, 1938.

DIAGNOSTIC FEATURES. Body small, oval. Body-surface covered with small spines, which are easily lost or overlooked. Cirrus-sac present; oval; well developed, but with thin wall; dorsal or antero-dorsal to ventral sucker. Seminal vesicle internal; large; bipartite. Pars prostatica short; surrounded by few gland-cells. Ejaculatory duct narrow. Cirrus normally papilla-like. Ovary oval to lobed; usually more or less inter-testicular. Laurer's canal long, narrow; opening at posterior extremity and dorsally to excretory pore. Canalicular seminal receptacle present. Vitellarium two symmetrical fields of a few clusters or masses of small follicles (these clusters may break up); lateral to ventral sucker and/or in forebody. Parasitic in stomach or intestine of marine or brackish water teleosts.

TYPE-SPECIES. *Bacciger bacciger* (Rudolphi, 1819) (by monotypy).

COMMENT. Only a single species of *Bacciger*, the type-species, has been recorded in our region. As the other species of the genus are not well known with regard to their detailed morphology, our conception of its diagnostic features are based mainly upon this species.

Of the nine species which have been assigned to this genus, we consider that there are only four which are probably valid. These are:

(1) *Bacciger bacciger* (Rudolphi, 1819) Nicoll, 1914; type-species of the genus (p. 250).
(2) *B. cochinensis* Hafeezullah & Siddiqi, 1970; from the intestine of *Thrissocles mystax* off India.
(3) *B. grandispinatus* Naidenova, 1970; from the intestine of *Mesogobius batrachocephalus* in the Azov Sea.
(4) *B. ovatus* (Price, 1934) comb. nov. [syns. *Steringotrema ovata* Price, 1934, *Fellodistomum ovatum* (Price) Yamaguti, 1971, *B. opisthonemae* Nahhas & Cable, 1964]; this species was first described from a single specimen from the pyloric caeca of *Opisthonema oglinum* off Puerto Rico. Nahhas & Cable (1964) described their new form, *B. opisthonemae*, from the caeca of the same host off Jamaica. As Nahhas & Cable pointed out, the two descriptions differ only slightly, and we believe that there can be little doubt that the two worms are conspecific. Price failed to see spines on the tegument; but these are frequently lost or overlooked in this genus. The different configurations of the testes and ovary are probably explained by flattening or misinterpretation. This species differs from other species of *Bacciger* in having longer caeca, and a genital pore which is submedian and much more anteriorly positioned.

The remaining five species are:

(1) *Bacciger harengulae* Yamaguti, 1938; this species was used as the type-species of the genus *Pseudobacciger* by Nahhas & Cable (1964).
(2) *B. melanostomum* Naidenova, 1970; from the intestine of *Neogobius melanostomus* in the Azov Sea. This species differs from *Bacciger* in having a pre-testicular uterus and a continuous band of vitelline follicles across the anterior hindbody. It has been suggested to us by Dr A. V. Gaevskaja (*in litt.*) that this species corresponds to '*Pentagramma*' *petrowi* (Layman, 1930) which occurs in the same host.
(3) *B. nicolli* Palombi, 1934; a synonym of *B. bacciger* (see p. 253).

(4) *B. petrowi* (Layman, 1930) Zhukov, 1959; now considered to be a species of *Pronoprymna* (see p. 259).
(5) *B. sardinellae* Hafeezullah & Siddiqi, 1970; from the intestine of *Sardinella fimbriata*, India. This species is possibly a member of the genus *Pronoprymna*.

Bacciger bacciger* (Rudolphi, 1819) Nicoll, 1914

Distoma baccigerum Rudolphi, 1819.
Distoma (*Dicrocoelium*) *baccigerum* (Rudolphi) Parona, 1912.
Dicrocoelium baccigerum (Rudolphi) Zernov, 1913.
(?) *Cercaria lata* Lespés, 1857.
(?) *Cercaria pectinata* Huet, 1891.
(?) *Cercaria lutea* (van Beneden) of Giard (1897).
Bacciger nicolli Palombi, 1934.
Pseudobacciger nicolli (Palombi) Yamaguti, 1971.
(?) *Ovotrema pontica* Pigulewsky, 1938.
(?) *Steringotrema* (*Ovotrema*) *ponticum* (Pigulewsky) Yamaguti, 1953.

TYPE-HOST AND LOCALITY. *Atherina hepsetus*, Naples, Italy.

RECORDS
(i) Material studied
(a) From the NE Atlantic
Atherina presbyter [stomach] Loch Maddy, North Uist, Outer Hebrides, Scotland (Nov., 1952) (see Margolis & Ching, 1965; as *B. nicolli*). Material lent by L. Margolis.
—— [stomach] Port Erin, Isle of Man, Irish Sea (July, 1960). BM(NH) 1977.9.30.2–7.
—— [stomach] Salcombe, Devon, England (Nov., 1967). BM(NH) 1977.9.30.1.
—— ['gut'] Solent, Hampshire, England. Collected by T. Reader. BM(NH) 1979.2.14.23.

(b) From elsewhere
None

(ii) NE Atlantic records from the literature
Atherina presbyter [stomach] North Uist, Outer Hebrides, Scotland (Nov., 1952). Margolis & Ching (1965 : 388; as *B. nicolli*).
—— [stomach] Plymouth, Devon, England. Nicoll (1914 : 481).

ASPECTS OF BIOLOGY. Records of the intra-molluscan stages, including cercariae, from the NE Atlantic region which are claimed to belong to *B. bacciger* are as follows:
Barnea candida. Boulogne, Artois, France. Giard (1897 : 954; as *Cercaria lutea*). Wimereux, Artois, France. Pelseneer (1906 : 163; 1926 : 39; as *Cercaria pectinata* (*lutea*)).
Donax trunculus. Wimereux, Artois, France. Pelseneer (1906 : 163; as *Cercaria pectinata*).
Donax vittatus. Wimereux, Artois, France. Giard (1897 : 95; as *Cercaria lutea*); Dollfus (1925 : 59; as *Cercaria pectinata*); Pelseneer (1926 : 33; as *Cercaria pectinata*).
—— St Efflam, Finistère, France. Matricon-Gondran (1971 : 319).
—— Burry Inlet, South Wales. James *et al.* (1977 : 13; as *Cercaria pectinata*).
Venerupis decussata. Saint Vaast-la-Hougue, Manche, France. Dollfus (1925 : 59; as *Cercaria pectinata*).
Venerupis pullastra. Arcachon, Gironde, France. Jobert (1894: 519; see Pelseneer, 1906; 13; as *Cercaria pectinata*).
—— Wimereux, Artois, France. Pelseneer (1906 : 163; as *Cercaria pectinata*).
—— Saint Vaast-la-Hougue, Manche, France. Dollfus (1925 : 59; as *Cercaria pectinata*).

---

* In using the specific name *bacciger*, rather than the original *baccigerum*, Nicoll (1914) appears to have treated it as an adjective and made it masculine. It is possible that the name is a lapsus for 'baccifer', meaning 'bearing berries', and might have referred to the follicular vitellarium which would have been visible to Rudolphi in uncleared specimens.

In addition to the authors listed above, the larval stages of what is thought to be *B. bacciger* have been extensively studied by Huet (1891), Palombi (1932; 1933; 1934*a*; 1934*b*; 1940), Dolgikh (1963; 1965*a*; 1966*a*; 1966*b*; 1968*a*; 1968*b*; 1970), Matricon-Gondran (1965; 1966) and Gaevskaja [née Dolgikh] (1972). The miracidium evidently enters the bivalve molluscan host, where it develops into a slender mother-sporocyst. This gives rise to a daughter-sporocyst (Yamaguti, 1975), within which the cercariae develop. The cercariae are gymnocephalous and possess both a setiferous tail and a spinulate body-surface. The metacercaria has been found in the amphipod *Erichthonius difformis*, within a thick-walled cyst, and has also been discovered still within the amphipod in the gut of *Atherina* spp. Whether all of the above records from molluscs are of *B. bacciger* is difficult, or impossible, to determine, at the present time; but the variety of bivalve genera represented among the hosts and the morphological similarity of the adults of many of the fellodistomids suggests that some confusion with other species, and especially with *Pronoprymna*, might have occurred. '*Cercaria pectinata*' has been studied in Korea by Chun & Lee (1976) and Bae, Kang & Kim (1977), but the latter authors appear to consider it to be a larval stage of *Bacciger harengulae*.

All of the records of the adult parasite from the NE Atlantic have been from *Atherina presbyter*; but elsewhere this species has been recorded in other species of *Atherina* and is also reported to occur in *Clupeonella*, *Boops*, *Sardina*, *Lutjanus*, *Sardinella*, *Engraulis* and *Alosa*, although some of these reports are questionable. Its distribution appears to follow that of *Atherina*, occurring in coastal waters in the NE Atlantic region from Britain south to North Africa, in the Mediterranean Sea and in the Black Sea. In addition, it has been recorded in the Red Sea (Parukhin, 1975, 1976).

PREVIOUS DESCRIPTIONS. Stossich (1888 : 101; 1889 : 27; as *Distomum baccigerum*); Nicoll (1914 : 481); Palombi (1933 : 1; 1934*a* : 438); Skrjabin & Koval (1957 : 193); Nikolaeva (1963 : 410); Margolis & Ching (1965 : 384; as *B. nicolli*).

DESCRIPTION (Fig. 14). Unfortunately, all but one of the specimens studied, 39 whole-mounts and 3 sets of serial sections, were taken from preserved fish, so that their condition, whilst adequate for description, was not good. The small, oval worm (Fig. 14a & b) bears, over its surface, small spines which are easily lost. The dimensions of this species are included in Table 10. The subterminal *oral sucker* is similar in size to the small and weakly developed *ventral sucker*, which lies just within the anterior half of the body. There is a short prepharynx, a globular and small *pharynx* and a distinct oesophagus of variable length. The intestinal bifurcation occurs just anteriorly to the anterior margin of the ventral sucker, and the short and narrow caeca normally reach back only to the anterior margins of the testes, although they occasionally do not reach the testes or reach back to the middle of these organs (Fig. 14a & b).

The *excretory pore* is terminal, and leads into a narrow, 'Y'-shaped vesicle which possesses a very short stem, so that in fact the vesicle is more or less 'V'-shaped. (We have referred to it as 'Y'-shaped in the Baccigerinae, although the stem is hardly any longer than in the cases of *Prudhoeus* and *Steringotrema*, which we have referred to as 'V'-shaped; but in the latter cases the arms are broad and as such reduce the size of the stem to insignificance as far as the total volume of the vesicle is concerned.) The narrow arms reach just into the forebody.

The *testes* are large, globular and symmetrical or almost symmetrical, lying immediately posterior or postero-lateral to the ventral sucker. The vasa efferentia pass through the muscular wall of the cirrus-sac separately but close together. The *cirrus-sac*, is broadly oval and occurs dorsally or dorso-laterally to the ventral sucker. It contains a large, bipartite seminal vesicle (Fig. 14c), a short and wide pars prostatica with few external gland-cells and a smooth lining, and a short and narrow ejaculatory duct which passes through a distinct, papilla-like cirrus. The cirrus is present in all of our sectioned specimens and lies at the base of a deep, narrow genital atrium, which opens in the median line almost immediately anterior to the anterior margin of the ventral sucker.

The *ovary* is irregularly oval, lying between the testes and either just posterior to or dorsal to the ventral sucker. The oviduct passes from the posterior margin and is almost immediately united with Laurer's canal (Fig. 14d). The latter canal is wide proximally and then becomes

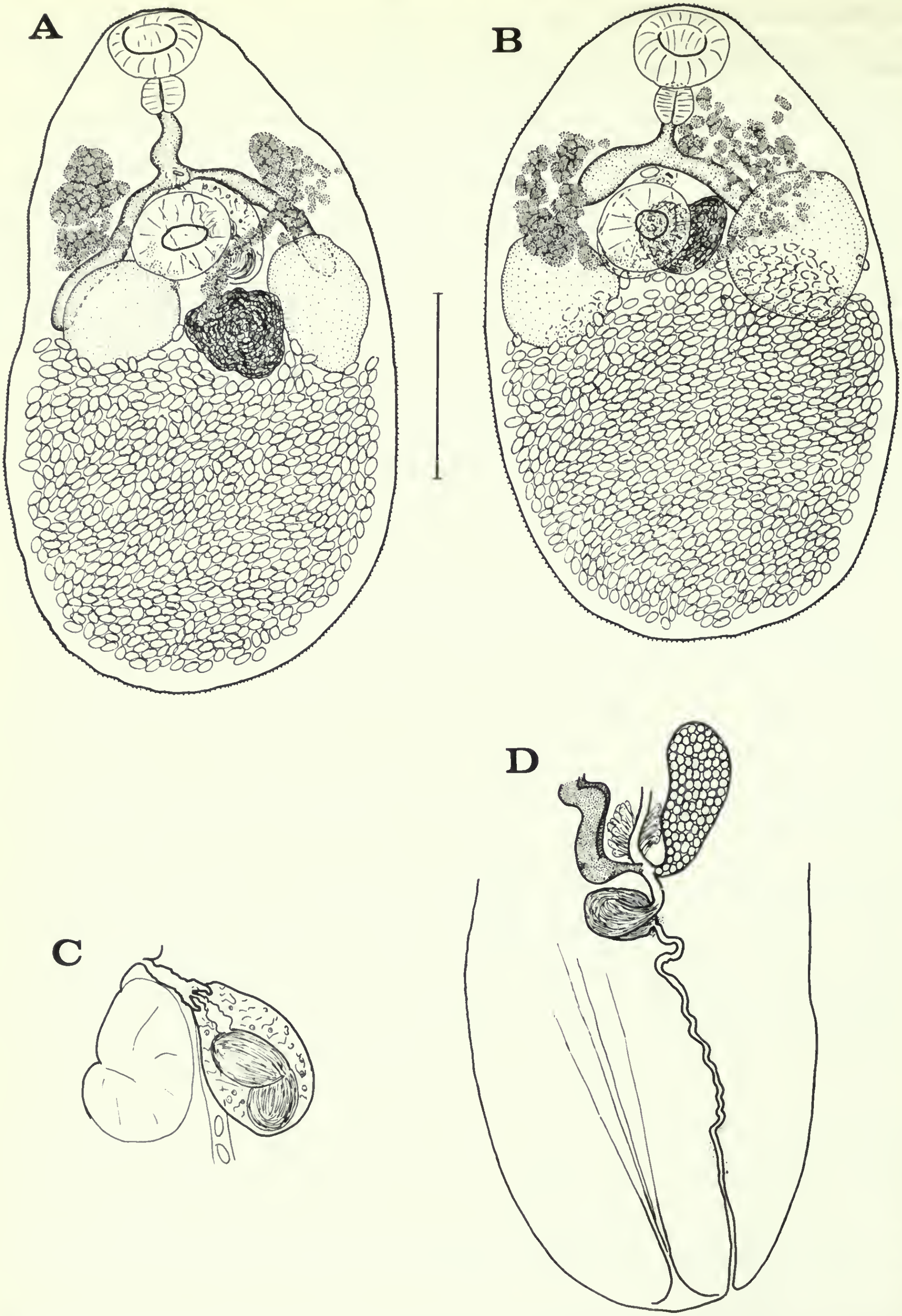


Fig. 14 *Bacciger bacciger:* (a) specimen from Salcome; (b) specimen from Port Erin; (c) cirrus-sac; (d) diagram of proximal female genitalia and part of excretory system. Bar scale: a, b = 0·2 mm.

Table 10 Dimensions of *Bacciger bacciger* from the present material and from the literature

Authority	Margolis & Ching (1965)	Margolis & Ching (1965)	Present material	Present material	Present material
Name used	*Bacciger bacciger*	*Bacciger nicolli*	*Bacciger bacciger*	*Bacciger bacciger*	*Bacciger bacciger*
Host	*Atherina hepsetus* *A. boyeri*	*Atherina presbyter*	*Atherina presbyter*	*Atherina presbyter*	*Atherina presbyter*
Locality	Black Sea, Naples	Outer Hebrides	Salcombe	Isle of Man	Solent
Length (mm)	0·59–0·90	0·72–1·08	0·81	0·48–0·64	0·87
Breadth (mm)	0·31–0·54	0·47–0·57	0·46	0·36–0·43	0·48
Length : forebody ratio	(1 : 0·26)	(1 : 0·29)	1 : 0·27	1 : 0·24–0·36	1 : 0·32
Oral sucker (mm)	0·071–0·13	0·10–0·13	0·11 × 0·75	0·087–0·105 × 0·070–0·075	0·07 × 0·11
Ventral sucker (mm)	0·066–0·097 × 0·11–0·13	0·13–0·15	0·115–0·10	0·095–0·13 × 0·090–0·094	0·13 × 0·12
Sucker-ratio	1 : 0·83–1·46	1 : 1·05–1·42	1 : 1·05	1 : 0·9–1·48	1 : 1·1
Pharynx (mm)	0·032–0·049 × 0·038–0·055	0·039–0·058	0·045 × 0·055	0·037–0·040 × 0·037–0·045	0·044 × 0·048
Oesophagus (mm)	0·065–0·12	0·039–0·097	0·065	0·060–0·082	–
Cirrus-sac (mm)	0·071–0·17 × 0·052–0·13	0·097–0·13 × 0·075–0·091	0·155 × 0·10	0·155 × 0·085	–
Testes (mm)	0·084–0·21	0·11–0·23	0·115–0·155 × 0·095–0·140	0·160–0·165 × 0·125	0·18–0·21 × 0·18
Ovary (mm)	0·10–0·15	0·10–0·17 × 0·074–0·17	0·105 × 0·095	0·10 × 0·13	0·13 × 0·14
Eggs (µm)	20–26 × 12–17	21–27 × 13–17	24–27 × 15–16	23–27 × 15–17	22–24 × 16–20

extremely wide just posterior to Mehlis' gland where it forms a large canalicular seminal receptacle. The distal extremity is delimited by a sphincter from which Laurer's canal, now narrow and convoluted, continues posteriorly through the middle of the uterine coils, and opens at the posterior extremity of the body just dorsally to the excretory pore (Fig. 14d). The distal region of the canal is almost straight. After receiving Laurer's canal the oviduct receives the common vitelline duct prior to passing through Mehlis' gland, which lies ventrally to the ovary. There is no uterine seminal receptacle. The *uterus* occupies much of the hindbody and almost the entire post-gonadal region and contains numerous operculate eggs. It is difficult to distinguish how the coils lie, but the distal region of the uterus passes anteriorly between the testes and unites with the base of the genital atrium beside the cirrus. The *vitellarium* is follicular, occurring in two lateral fields which lie between the level of the pharynx and the level of the posterior margin of the ventral sucker. The normal arrangement is apparently for the small follicles to clump together in three or four distinct masses (Fig. 14a); but in most of our material these masses have broken down and the individual follicles are scattered around the area (Fig. 14b). The vitellarium feeds two wide lateral collecting ducts which pass postero-medially towards the ovary, ventral to which they unite to form the common vitelline duct. This short duct is dilate proximally, forming a small vitelline reservoir. The lateral vitelline ducts are usually a prominent feature in the preserved worm.

Discussion. The specimens described by Nicoll (1914) from Plymouth were considered by Palombi (1934*a*) to belong to a species distinct from *Bacciger bacciger* as it is known in the Mediterranean and Black Seas, and the name *B. nicolli* was given to it. Margolis & Ching (1965) record the only other previous finding of this species in the northeast Atlantic, and describe worms which are much closer to *B. bacciger* than Nicoll's description. They argue, however, that the northeastern Atlantic form (*B. nicolli*) is distinct from *B. bacciger* on two grounds: (1) they point out that it has been found only in the stomach of *Atherina presbyter*, whilst the Mediterranean/Black Sea form is only found in the intestine of its hosts; and (2) they indicate that the shape of the ovary, which is more or less lobed in *B. nicolli*, is entire in *B. bacciger*. However, dealing with the last point, we have found that the shape of the ovary of fellodistomids is constant in well-fixed, unflattened mature worms; but in immature worms or in poorly fixed or flattened adults the shape may be indistinct or the outline may break down. It should, therefore, be stressed that most of the material studied from the northeast Atlantic was taken from preserved fish, and Nicoll's specimens were from fishes in which 'the viscera were somewhat decomposed and the parasite badly preserved'. Hence, it would appear that the shape of the ovary is not a satisfactory differentiating character in this instance. The difference in the location of the parasite in the host does suggest a biological distinction; but, in connection with this, it would be interesting to know what the status of the stomach of *Atherina presbyter* is in relation to the physiologically stomach-less fishes mentioned by Barrington (1957). Further doubt is cast upon this distinction by the recent report of *B. bacciger* from the 'stomach' of *Boops boops* in the Adriatic Sea by Sey (1970) and of various fishes in the Mediterranean and Red Seas by Parukhin (1971, 1976). In retrospect, therefore, we do not believe that at the present time there is sufficient evidence to recognize *B. nicolli* as a distinct species.

Yamaguti (1971) included *B. nicolli* in the genus *Pseudobacciger* Nahhas & Cable, 1964. We are at a loss to comprehend this, as both published descriptions of this species clearly indicate the presence of a *cirrus-sac*!

Skrjabin & Koval (1957) suggest that *Ovotrema pontica* Pigulewsky, 1938, from the intestine of *Engraulis encrasicolus* in the Black Sea is a synonym of *B. bacciger*. This synonymy was discounted by Margolis & Ching (1965). The poor description of this species does show, however, a gross morphology similar to the baccigerines and fellodistomines. Since Pigulewsky's work both *B. bacciger* and *Pronoprymna ventricosa* have been recorded from the type-host and locality of this species, i.e. *B. bacciger* (Koval, in Skrjabin & Koval, 1957; Nikolaeva, 1963); and *P. ventricosa* (Nikolaeva, 1963). Of the two, *O. pontica* appears to be most similar to *B. bacciger*, although differing significantly in the submedian position of the genital pore and in the large size of the ventral relative to the oral sucker. When compared to the figure of *B. bacciger* from the same host and locality given by Koval, in Skrjabin & Koval (1957), however, the difference in the transverse sucker ratios, as shown in Pigulewsky' figure, is less significant. As one cannot always take inadequate descriptions at face value and because of the more recent circumstantial evidence, we accept *O. pontica* as a questionable synonym of *B. bacciger*. This species is also discussed on p. 233 and p. 259.

Genus ***PRONOPRYMNA*** Poche, 1926

Pentagramma Chulkova, 1939, *nec* Van Duzee, 1897.
Pseudopentagramma Yamaguti, 1971.

DIAGNOSTIC FEATURES. Body small, fusiform. Body-surface smooth. Cirrus-sac elongate; thin-walled; closely applied to surface of seminal vesicle. Seminal vesicle internal; bipartite. Pars prostatica short; surrounded by few gland-cells. Ejaculatory duct short. Cirrus absent as a permanent structure. Ovary median; post-testicular; irregularly trilobed. Laurer's canal opening on dorsal surface close to posterior extremity. Canalicular seminal receptacle present. Vitellarium two symmetrical compact masses composed of small follicles; masses may occasionally be dispersed; lateral or just posterior to ventral sucker. Parasitic in intestine, caeca and (?) stomach of marine teleosts.

TYPE-SPECIES. *Pronoprymna ventricosa* (Rudolphi, 1819) (by original designation).

COMMENT. The name *Pronoprymna* was introduced by Poche (1926) as a replacement name for *Pronopyge* Looss, 1899. Looss (1899) had erected and defined *Pronopyge*, quoting the type as being '*Pronopyge ocreata* (Rud.) (= *Dist. carolinae* Stossich)', and in the definition and a footnote had made it clear that he was using the description of '*Apoblema ocreatum*' by Monticelli (1891), which is clearly of a fellodistomid, in formulating his conception. Monticelli (1891) included not only *D. carolinae*, but also *D. ventricosum* Rudolphi, 1819, as a synonym of his '*Apoblema ocreatum*'. The history of *Distoma ocreatum* is rather involved and will be discussed in more detail elsewhere when discussing *Hemiurus luehei* Odhner, 1905 (Gibson & Bray, in preparation), but its early records are from the stomach and intestine of *Clupea harengus* and Rudolphi (1809), the author of the name, makes it clear that it is an appendiculate (ecsomate) form. Molin (1861) described '*Distoma ocreatum* Rudolphi' from the stomach of *Alosa alosa* at Venice, and then Monticelli (1891) presented his description of '*Apoblema ocreatum*' from the stomach of an 'alose' dissected at Naples. Odhner (1911*b* : 528 footnote) was unable to understand why Monticelli (1891) considered *D. ocreatum* and *D. ventricosum* synonymous, and, on a re-examination of Rudolphi's specimens, declared that *D. ocreatum* of Rudolphi belongs to the genus *Hemiurus* Rudolphi, 1809, and is in fact synonymous with his own species *H. luehei*.

Distoma ventricosa was originally recorded by Rudolphi (1819) from the intestine (p. 108) or stomach (p. 398) of *Alosa alosa* at Rimini. Odhner (1911*b*) also re-examined the types of this species and was convinced that they were a species of '*Pronopyge*'. The type-species of the genus *Pronopyge*, however, was originally designated as *P. ocreata* (Rud.), and, as Article 42(b) of the ICZN makes clear, the genus is 'objectively defined only by reference to its type-species' and that (Article 70) 'it is to be assumed that an author correctly identifies the nominal species that he . . . designates as the type-species of the new or of an established genus'. Poche (1926), anticipating these provisions of the ICZN, produced the new name *Pronoprymna* with the type-species *Distoma ventricosum* Rud., which, it appears, must stand as the valid name of this genus. In short, although Looss' concept of *Pronopyge* is the same as Poche's of *Pronoprymna*, the name *Pronopyge* is objectively based on Rudolphi's *D. ocreatum*, which is now known to be a *Hemiurus* and, therefore, automatically becomes a synonym of the latter genus.

An examination of the description of Molin (1861; as *Distoma ocreatum*) and Monticelli (1891 ; as *Apoblema ocreatum*: Looss' conception of *Pronopyge* is based upon this description), and a comparison with our own material, shows that we are dealing with a fellodistomid genus close to *Bacciger*. It must be more than a coincidence that Rudolphi (1819) described *Distoma ventricosum* and *D. baccigerum* next to one another. It is also apparent that the same species has been figured by van Beneden (1871), who called it *Distoma ventricosa* (p. 68) and *D. ventricosum* (p. 69), and by Stossich (1888, 1889) under the name *Distomum carolinae*. The latter two records are from *Alosa fallax* (=*finta*) off the Belgian coast and Trieste, respectively. The picture of this species that is built up from these various descriptions and figures indicates that it is the same species as was described under the name *Pentagramma symmetricum* by Chulkova (1939) and Margolis & Ching (1965) from shads in the Black Sea and as *Orientophorus caspialosae* by Kurochkin (1964) from shads in the Caspian Sea. The name *Pentagramma carolinae* (Stossich) has been used for specimens from the Black Sea region by Koval *et al.* (1973). *Pentagramma* Chulkova, 1939, is pre-occupied and has been replaced by *Pseudopentagramma* Yamaguti, 1971; but both of these names now become synonyms of *Pronoprymna*.

There appear to be two known valid species of the genus *Pronoprymna*. These are:

(1) *Pronoprymna petrowi* (Layman, 1930) n. comb. [syns. *Monorcheides* (?) *petrowi* Layman, 1930; *Orientophorus petrowi* (Layman) Mamaev, Parukhin, Baeva & Oshmarin, 1959; *Bacciger petrowi* (Layman) Zhukov, 1959; *Pentagramma petrowi* (Layman) Margolis & Ching, 1965; *Pseudopentagramma petrowi* (Layman) Yamaguti, 1971; *Orientophorus sayori* Yamaguti, 1942; *Faustula sayori* (Yamaguti) Yamaguti, 1958]; from various fishes, notably clupeids, from the North Pacific. This species is reviewed by Margolis & Ching (1965). See also p. 259).

(2) *P. ventricosa* (Rudolphi, 1891) Poche, 1926; type-species of the genus (see below).

Pronoprymna ventricosa (Rudolphi, 1819) Poche, 1926

Distoma ventricosum Rudolphi, 1819.
Apoblema ventricosum (Rudolphi) Monticelli, 1893.
Pronopyge ventricosa (Rudolphi) Odhner, 1911.

Distoma ocreatum (Rudolphi) of Molin (1859; 1861)
Apoblema ocreatum (Rudolphi) of Monticelli (1891).
Pronopyge ocreata (Rudolphi) of Looss (1899).
Distomum carolinae Stossich, 1888.
Pronopyge carolinae (Stossich) Dollfus, 1968.
Pentagramma carolinae (Stossich) Koval, Paschkevitschute, Boschko, Kovalenko & Stavrovsky, 1973.
Pentagramma symmetricum Chulkova, 1939.
Pseudopentagramma symmetricum (Chulkova) Yamaguti, 1971.
Orientophorus caspialosae Kurochkin, 1964.
Pseudopentagramma caspialosae (Kurochkin) Yamaguti, 1971.

TYPE-HOST AND LOCALITY. *Alosa alosa*, Rimini, Italy.

RECORDS

(i) Material studied

(a) From the NE Atlantic

Alosa alosa [pyloric caeca] SW Irish Shelf, Celtic Sea (Dec., 1974). Donated by A. V. Gaevskaja. BM(NH) 1978.2.22.1–2.

Alosa fallax [intestine] River Severn, England (May). Collected by C. R. Kennedy. BM(NH) 1977.10.11.1–20.

—— [?] Scarborough, North Yorkshire, England (Jan., 1978). Collected by D. Whittaker. BM(NH) 1979.2.14.20–22.

(b) From elsewhere

Alosa pontica [?] Black Sea (1968). Studied for us by A. V. Gaevskaja.

Engraulis encrasicolus [pyloric caeca] Black Sea. Collected by V. M. Nikolaeva. Material of L. Margolis.

(ii) NE Atlantic records from the literature

Alosa alosa [intestine] Belgian coast. van Beneden (1871 : 69; as *Distoma ventricosum*, but not figured or described).

—— [stomach, intestine] River Rhine at Basle, Switzerland. Zschokke (1896 : 775; as *Distomum ventricosum*, but not figured or described); Hausmann (1897 : 6, 20; as *D. ventricosum*, but not figured or described).

Alosa fallax [stomach] Belgian coast. van Beneden (1871 : 68; as *Distoma ventricosa*, figured).

Sprattus sprattus [pyloric caeca, intestine] Belgian coast. van Beneden (1871 : 67; as *Distoma ventricosum*, but not figured or described).

ASPECTS OF BIOLOGY. Nothing is known of the life-history of this worm. It appears to be a relatively common parasite of shads (*Alosa* spp.) and occurs less commonly in other fishes, notably other clupeids. It is found in the Mediterranean, Black and Azov Seas, as well as in the NE Atlantic region, and is said to occur in the South Atlantic and Red Sea (Parukhin, 1975).

PREVIOUS DESCRIPTIONS. Molin (1861 : 209; as *Distoma ocreatum*); van Beneden (1871 : plate IV, Fig. 11; as *Distoma ventricosum*); Stossich (1888 : 101; 1889 : 26; as *Distomum carolinae*); Monticelli (1891 : 508, as *Apoblema ocreatum*); Chulkova (1939 : 22; as *Pentagramma symmetricum*); Nikolaeva (1963 : 411; as *P. symmetricum*); Kurochkin (1964 : 166; as *Orientophorus caspialosae*); Margolis & Ching (1965 : 391; as *P. symmetricum*); Naidenova (1970 : 95; as *P. symmetricum*).

DESCRIPTION (Fig. 15). This description is based upon 33 whole-mounted and 7 sectioned specimens. Our observations have been supplemented by measurements and figures of specimens from both the Celtic Sea and Black Sea carried out by Dr Gaevskaja. The worms are small and have a fusiform outline (Fig. 15a & b); the dimensions are given in Table 11. As far as could be ascertained the surface of the body is smooth and does not bear spines. The subterminal, globular *oral sucker* is usually slightly smaller than the globular *ventral sucker*, which is present just inside the anterior half of the worm. There is a short prepharynx, a small, oval *pharynx* and a distinct oesophagus, which is longer than the pharynx. The caecal bifurcation occurs in the posterior forebody, and the narrow caeca reach back dorso-laterally to just beyond the testes where they end blindly.

The *excretory pore* is terminal. It leads into a vesicle which is essentially 'V'-shaped, although it has a short, narrow stem. The arms reach into the forebody to about the level of the oesophagus.

The irregularly oval to globular *testes* lie symmetrically in the anterior half of the hindbody. The vasa efferentia enter the cirrus-sac separately, but close together, The *cirrus-sac* is elongate oval, lying dorsally or dorso-laterally to the ventral sucker. Its thin wall adheres closely to the surface of a large, internal, bipartite seminal vesicle, the posterior part of which is usually the larger (Fig. 15c). The pars prostatica is short, difficult to differentiate, in fact it is almost non-existent, and there are a few external gland-cells. The ejaculatory duct is also short, and we found no evidence that a cirrus is formed, as occurs in *Bacciger*. The ejaculatory duct opens into the base of a long, narrow genital atrium (Fig. 15c); some authors have regarded this as part of the ejaculatory duct. The genital pore opens just anteriorly to the ventral sucker, and is more or less median, although it may be displaced slightly in some specimens.

The *ovary* lies in the median line just posterior to the testes. It is trilobed, although the lobes may be somewhat irregular and the lobation is often not clearly visible in poorly preserved material, or the whole ovary may be obscured by eggs. The short oviduct leaves the ovary ventrally and almost immediately receives Laurer's canal (Fig. 15d) and the common vitelline duct. The proximal region of Laurer's canal is dilated to form a canalicular seminal receptacle

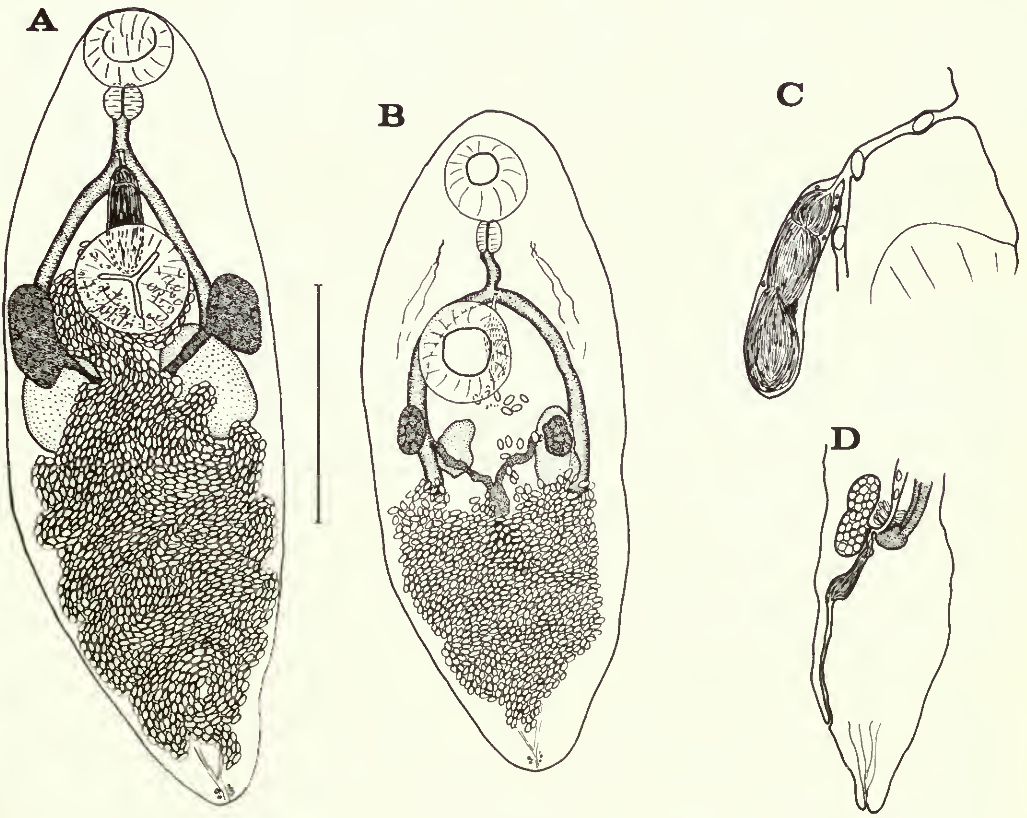


Fig. 15 *Pronoprymna ventricosa:* (a) specimen from Celtic Sea; (b) specimen from River Severn; (c) cirrus-sac; (d) diagram of female proximal genitalia and part of excretory system. Bar scale: a, b = 0·5 mm.

posterior to the ovary. It then continues posteriorly dorsal to the uterine field, before opening to the exterior on the dorsal surface close to the posterior extremity. There is no uterine seminal receptacle. The *uterus* fills most of the hindbody posterior to the testes and contains numerous operculate eggs. It is not possible to discern how the uterus coils, but the narrow distal region passes anteriorly between the testes and dorsal or dorsolateral to the ventral sucker, and unites with the ejaculatory duct at the base of the narrow genital atrium (Fig. 15c). The *vitellarium* consists of two symmetrical masses of tightly packed follicles, lying laterally or postero-laterally to the ventral sucker. Occasionally the follicles are dispersed, and more often only on one side: this effect occurs much more frequently in poorly preserved material. The thick main vitelline collecting ducts form a conspicuous 'V'-shaped structure in the middle of the body, the ducts meeting ventrally or antero-ventrally to the ovary to form a distinct vitelline reservoir of variable size (Fig. 15b & d). This reservoir is the dilated common vitelline duct.

Table 11 Dimensions of *Pronoprymna ventricosa* from the present material and from the literature

Authority	Margolis & Ching (1965)*	Gaevskaja (in litt.)	Present material	Present material	Present material
Name used	*Pentagramma symmetricum*	*Pentagramma symmetricum*	*Pronoprymna ventricosa*	*Pronoprymna ventricosa*	*Pronoprymna ventricosa*
Host	*Engraulis encrasicolus*	*Alosa pontica*	*Alosa fallax*	*Alosa alosa*	*Alosa fallax*
Locality	Black Sea	Black Sea	River Severn	Celtic Sea	Scarborough
Length (mm)	0·41–0·94	1·02–1·56	1·24–1·80	1·30–1·66	1·3–1·4
Breadth (mm)	0·17–0·32	0·34–0·36	0·40–0·74	0·51–0·67	0·43–0·48
Length : forebody ratio	1 : 0·26–0·31	(1 : 0·30)	1 : 0·24–0·30	1 : 0·25–0·27	1 : 0·25–0·27
Oral sucker (mm)	0·071–0·094; 0·09–0·10 × 0·08–0·10	0·13–0·15 × 0·15–0·16	0·13–0·20 × 0·15–0·17	0·12–0·17 × 0·14–0·18	0·11–0·15 × 0·14–0·16
Ventral sucker (mm)	0·09–0·12; 0·09–0·14 × 0·10–0·12	0·18–0·20 × 0·18–0·20	0·13–0·23 × 0·14–0·24	0·15–0·25 × 0·17–0·23	0·16–0·18 × 0·14–0·20
Sucker-ratio	1 : 1·1–1·25	(1 : 1·5)	1 : 0·9–1·3	1 : 1·02–1·20	1 : 1–1·25
Pharynx (mm)	0·039 × 0·029–0·039	0·059 × 0·051	0·055–0·060 × 0·060–0·077	0·07–0·10 × 0·06–0·07	0·05–0·08 × 0·05–0·06
Oesophagus (mm)	0·026–0·030	0·046–0·059	0·13–0·15	0·10–0·13	0·06–0·07
Cirrus-sac (mm)	–	–	–	0·14–0·23 × 0·05–0·07	0·18–0·25 × 0·05–0·07
Testes (mm)	0·071–0·15 × 0·066–0·11	0·11–0·16 × 0·081–0·12	0·18 × 0·13–0·15	0·20–0·29 × 0·17–0·21	0·17–0·22 × 0·10–0·17
Ovary (mm)	0·075–0·13; 0·13–0·12	0·16 × 0·12–0·15	–	–	–
Eggs (µm)	20–32 × 14–18	27 × 14	26–33 × 16–18	27–30 × 16–18	23–28 × 16–18

* These data include our measurements of Margolis' material.

DISCUSSION. The description above agrees closely with that of Margolis & Ching (1965) except for the interpretation of the terminal genitalia. The latter authors, when describing *Pentagramma petrowi*, considered that the ejaculatory duct is long and thin, did not apparently detect the union with the uterus at the base of the genital atrium, and thus seem to have confused the ejaculatory duct and the genital atrium. The early descriptions of Monticelli (1891) and Stossich (1889) show minor discrepancies with ours, but we have little doubt that these descriptions refer to the same species. The length of the caeca shown in the figures of these two workers is rather puzzling;

but, as in all of our whole-mounts the posterior extent of the caeca is obscured by eggs, it is likely that Monticelli and Stossich misinterpreted these structures. In some of the early descriptions, and in Looss' (1899) definition of *Pronopyge*, a small, button-shaped ecsoma is referred to; but an examination of the figures of Molin (1861) and Monticelli (1891) suggest that this is nothing more than a small protrusion surrounding the excretory pore: such a protrusion is visible in a number of the specimens from the Celtic Sea which we have examined.

Pronoprymna petrowi (Layman, 1930) is similar to *P. ventricosa*. Margolis & Ching (1965) cite three distinguishing features: sucker-ratio, position and shape of oral sucker, and position of seminal vesicle relative to ventral sucker. The combination of these three features, particularly the first two, would appear to constitute, at the present time, sufficient reason for recognizing both species although it is apparent that well-preserved specimens of the two species have not been compared in detail. Margolis & Ching suggested that there is a discontinuous distribution in the genus, with *P. ventricosa* in the Black and Azov Seas and *P. petrowi* in northern Pacific waters. The reports of *P. ventricosa* in the Mediterranean Sea and northeast Atlantic (see above), the Red Sea and South Atlantic (Parukhin, 1975), and of *P. petrowi* in the Black Sea (Naidenova, 1974) and Indian waters (Madhavi, 1975), questionable though some of these records are, decrease the likelihood that geographical isolation actually occurs.

Distoma catervarium Looss, 1896, for which Yamaguti (1971) erected the genus *Walliniella*, from the intestine of *Alosa fallax* at Cairo, is superficially similar to *P. ventricosa* and comes from one of its normal hosts. These parasites were, according to Looss (1896), poorly preserved, and it is possible, therefore, that certain of the features were misinterpreted. The supposedly post-ovarian testes, however, preclude our adding this name to the synonymy of *P. ventricosa*.

Ovotrema pontica Pigulewsky, 1938, from the intestine of *Engraulis encrasicolus* in the Black Sea, is also morphologically similar to *P. ventricosa*. It differs, however, from specimens of *P. ventricosa*, which we have examined from the same host in the Black Sea, in that it apparently possesses a dispersed, follicular vitellarium not extending into the hindbody, a submedian genital pore, and oval ovary and no distinct oesophagus. This species has been discussed on pages 233 and 254.

Subfamily **XENOPERINAE** Poche, 1926 *stat. emend.*

Proctoecinae Skrjabin & Koval, 1957.

DIAGNOSTIC FEATURES. Body small to medium-sized; cylindrical to oval, but widest at level of ventral sucker. Body-surface smooth. Oral sucker subterminal; normally smaller than ventral sucker. Ventral sucker inside anterior half of body. Prepharynx short. Pharynx large; oval to globular. Oesophagus short to apparently absent. Intestinal bifurcation in forebody. Caeca extending to or near to posterior extremity. Testes two; tandem to oblique; in mid-hindbody. Cirrus-sac elongate-oval; usually in hindbody or dorsal to ventral sucker. Seminal vesicle tubular, coiled; partly or entirely internal. Pars prostatica long, wide, filling much of cirrus-sac; with filamentous lining and many external gland-cells. Ejaculatory duct short; muscular; may form cirrus capable of great extension; muscular genital papilla present lateral to opening of male duct at base of genital atrium. Genital atrium long, narrow. Genital pore sinistrally or dextrally submedian in mid- to posterior forebody. Ovary globular to slightly lobed; pre-testicular in anterior hindbody; median to sinistral. Laurer's canal present; opening dorsally at level of gonads. Uterine seminal receptacle (?) presumed present. Canalicular seminal receptacle apparently absent. Uterus coiled mainly posterior to ovary, reaching to posterior extremity, opens into base of genital atrium immediately posterior to, at level of or immediately anterior to ventral sucker through long, muscular metraterm. Eggs numerous; small, but variable in size and shape; operculate. Vitellarium composed of elongate follicles, which may break down into small globular follicles or become inconspicuous; in two symmetrical, mainly lateral fields; in mid-hindbody or anterior to mid-hindbody. Excretory vesicle 'Y'-shaped, bifurcating in mid-hindbody; arms reaching to level of pharynx. Parasitic progenetically in marine molluscs or in intestine of marine teleosts (usually sparids or labrids).

COMMENT. When Nicoll (1915*b*) erected the genus *Xenopera* he considered it to be a hemiurid mainly because of the 'long tube-like genital sinus'; but he states that 'it cannot be considered by any means a typical member of the family'. Poche (1926) erected the family Xenoperidae in the superfamily Hemiurida [= Hemiuroidea], and this family was later placed in the suborder Hemiurata by Skrjabin & Guschanskaja (1956), but the latter authors subsequently (1958) considered it to belong to the suborder Azygiata. Dollfus (1952) drew attention to the similarities between *Xenopera* and the genus *Proctoeces* Odhner, 1911, and synonymized the two: much earlier, in 1925, in a hand-written note on his translation of Fujita (1925) held in the reprint collection of the Parasitic Worms Section, British Museum (Natural History), he stated, '*Proctoeces* Odhner 1911 = *Xenopera* Nicoll 1915'. When this parallel was drawn it was realized that the family Fellodistomidae was the most appropriate place for both *Xenopera* and *Proctoeces*. Skrjabin & Koval (1957) believed that *Gauhatiana* Gupta, 1955, *Mesolecitha* Linton, 1910, *Symmetrovesicula* Yamaguti, 1938, and *Urorchis* Ozaki, 1927, belonged to the Proctoecinae, a new subfamily of fellodistomids, but did not include *Xenopera*. However, Caballero y C. (1959), in raising the Proctoecinae to the family-rank, included the Xenoperidae as a synonym.

The name given to this subfamily depends upon the validity of *Xenopera* as a genus distinct from *Proctoeces*, as the family-group name based upon *Xenopera* is older than that based upon *Proctoeces*. *Xenopera* was erected for a new species, *X. insolita*, from the rectum of *Sparus australis* off Queensland, Australia, which Nicoll (1915*b*) described from five specimens. It is widely reckoned to be similar to *Proctoeces*, differing only in the possession of an external seminal vesicle. Some authors have, however, cast doubt upon Nicoll's observations, and both Dollfus (1952), as mentioned above, and Yamaguti (1958) have considered *Xenopera* to be a synonym of *Proctoeces*. Furthermore, *X. insolita* was considered by Freeman (1963*a*) to be a synonym of *P. subtenuis* (Linton, 1907), since, when examining many specimens of the latter species, he claimed to have found one with an external seminal vesicle. Freeman & Llewellyn (1958) described and figured *P. subtenuis*, and showed that the vasa efferentia unite at the point of entry into the cirrus-sac, and descriptions of *P. maculatus* (Looss, 1901) and its synonyms (Stunkard & Uzman, 1959; Loos-Frank, 1969; Lang & Dennis, 1976) also show that an unmodified vas deferens is either short or absent. Fujita's (1925) description of a metacercaria, *P. ostreae* from *Ostrea gigas* off Japan, shows the vasa efferentia uniting at the level of the anterior testis to form a vas deferens. If this became dilated with spermatozoa, it could form an external seminal vesicle, as in *Xenopera*. Dollfus, however, in a hand-written note on the reprint (see above) of Fujita's paper, of which he was the translator, stated, 'l'adulte de *P. ostreae* Fujita et Dollfus est peut être *Xenopera insolita* Nicoll (1915)'. A short vas deferens is also evident in *P. maculatus* as figured by Prevot (1965); but it is most unlike the prominent, coiled external seminal vesicle which Nicoll described in *Xenopera*.

The only other record of *Xenopera* is that of Manter & Pritchard (1962), who figured and briefly described a single specimen from an unidentified host in New Zealand and mentioned this worm '... only to verify the genus *Xenopera*'. Their figure shows that a distinct tubular, convoluted external seminal vesicle is present. It appears to us, therefore, that it is most likely that the possession of a long, convoluted external seminal vesicle is the normal condition in *Xenopera*, whereas, if it occurs, it is an unusual and less significant feature in *Proctoeces*. In contrast with the workers who synonymized *Xenopera* with *Proctoeces*, and with Dollfus (1965) who considered it to be a subgenus of *Proctoeces*, we prefer, until more is known about it, to accept *Xenopera* as being generically distinct, and accept the name Xenoperinae as the emended name of this subfamily.

Our concept of the subfamily Xenoperinae is based upon the genera *Xenopera* and *Proctoeces* and, in our opinion, the most important diagnostic features are the deep, narrow and extensible genital atrium, the convoluted, tubular seminal vesicle, and probably the presence of a muscular genital papilla in the base of the genital atrium beside the aperture of the male duct. As the subfamily is not well established, we have compared the data in the literature for all of the genera included in the Proctoecinae (-idae) by Skrjabin & Koval (1957) and Caballero y C. (1959), and they all lack some or all of these diagnostic features. We have, therefore, not included these genera in our concept of the subfamily.

The species of the genus *Gauhatiana* Dayal & Gupta, 1954 [originally spelt *Gauhatinae*] have been described by Gupta (1955) and Gupta & Miglani (1976). They differ from the Xenoperinae in having a spiny tegument (? lost in *G. lebedevi* Gupta & Miglani, 1974), a 'Y'-shaped excretory vesicle with short arms and a seminal receptacle. Skrjabin & Koval (1966) considered *Gauhatiana* a member of the family Walliniidae, but later (1974) omitted it from this family. Gupta & Miglani (1974, 1976) considered the genus to be a macroderoidid; but there seems no reason to disagree with Yeh & Fotedar (1958), who believed it to be a synonym of the plagiorchiid genus *Astiotrema* Looss, 1900, making *G. batrachii* Dayal & Gupta 1954, a synonym of *A. reniferum* (Looss, 1898).

The species of *Mesolecitha* Linton, 1910, have been described by Linton (1910), Manter (1947), Siddiqi & Cable (1960) and Fischthal & Thomas (1968). This genus lacks the diagnostic features of the subfamily and possesses a seminal receptacle, spines on both the cirrus and the metraterm and Linton (1910) and Fischthal & Thomas (1968) describe the tegument as finely spined. The correct systematic position of this genus is problematical.

The single species of *Symmetrovesicula* Yamaguti, 1938, has been described by Yamaguti (1938, 1953*b*). It lacks the diagnostic features of this subfamily and probably fits into the Fellodistominae, differing from the other genera of the latter group in possessing rosette-shaped clusters of vitelline follicles, an intestinal bifurcation in the hindbody and a 'V'-shaped excretory vesicle with wide arms.

The species of *Urorchis* Ozaki, 1927, have been described by Ozaki (1927), Yamaguti (1934, 1942) and Ishii (1935). Despite these four descriptions, there appears to be some confusion as to the shape of the seminal vesicle and the excretory vesicle. It appears, however, that the normal situation is a bipartite seminal vesicle and an I-shaped excretory vesicle, the latter being unknown in the Fellodistomidae. It also lacks the distinctive pars prostatica which occurs in the majority of the fellodistomids. Yamaguti (1942) considered it to be an allocreadiid genus, then later (1958) erected the allocreadiid subfamily Urorchiinae for it.

The only genus in our concept of this subfamily to occur in the north-east Atlantic region is *Proctoeces*.

Genus ***PROCTOECES*** Odhner, 1911

DIAGNOSTIC FEATURES. External seminal vesicle absent. Vasa efferentia unite at, or close to, base of cirrus-sac.

TYPE-SPECIES. *Proctoeces maculatus* (Looss, 1901) (by subsequent designation: Fujita, 1925 : 56).

COMMENT. Fourteen species have been assigned to this genus, seven of which we believe to be synonymous with the type-species. We consider the status of the others as follows:

(1) *Proctoeces insolitus* (Nicoll, 1915) Yamaguti, 1953; the type-species of the genus *Xenopera* Nicoll, 1915 (see above).

(2) *P. lintoni* Siddiqi & Cable, 1960; from sparid and labrid fishes in and around the Caribbean Sea. This species differs from *P. maculatus* in having a globular posterior portion in addition to the convoluted, tubular part of the seminal vesicle.

(3) *P. macrovitellus* Winter, 1954; it was pointed out by Freeman & Llewellyn (1958) that this was not a *Proctoeces*, and Winter later (1960) transferred it to the zoogonid genus *Diplangus* Linton, 1910.

(4) *P. magnorus* Manter, 1940; from *Caulolatilus anomalus* off the Pacific Coast of Mexico. This species is known only from a single specimen in which the oral sucker is larger than the slightly pedunculate ventral sucker. In addition to these features, it differs from *P. maculatus* in apparently possessing a smaller average egg-size (32–37 × 15–19 μm). Nevertheless, Freeman & Llewellyn (1958) considered it to be a synonym of *P. subtenuis* (Linton, 1907) [=*P. maculatus*]. In view of the differences listed above and until more material has been examined from the type-host and locality, we prefer to consider this species a *species inquirendum*.

(5) *P. neomagnorus* Siddiqi & Cable, 1960; this is considered a synonym of *Mesolecitha linearis* Linton, 1910, by Nahhas & Cable (1964).

(6) *P. ostreae* Fujita, 1925; described as a metacercaria which may be progenetic from the gonads of the bivalve *Crassostrea gigas* off Japan. It is said to occur as an adult in *Pagrosomus major* and *Epinephelus akaara* (Korringa, 1952), but Komiya (1965) believed that the final host was still unknown. Dollfus (see above) considered that it was possibly the metacercaria of *Xenopera insolita*.

Proctoeces maculatus (Looss, 1901) Odhner, 1911

Distomum maculatum Looss, 1901.
Distomum subtenue Linton, 1907.
Proctoeces subtenuis (Linton) Hanson, 1950.
Proctoeces erythraeus Odhner, 1911.
(?) *Proctoeces major* Yamaguti, 1934.
(?) *Cercaria tenuans* Cole, 1935.
Cercaria milfordensis Uzman, 1953.
Proctoeces progeneticus Dollfus, 1965.
Proctoeces sp. of Ichihara (1964, 1965).
Proctoeces buccini Loos-Frank, 1969.
Proctoeces scrobiculariae Loos-Frank, 1969.
Proctoeces hawaiiensis Yamaguti, 1970.

TYPE-HOST AND LOCALITY. *Labrus merula*, Trieste, Adriatic Sea.

RECORDS. All records from the NE Atlantic are from molluscs.

(i) Material studied

(a) From the NE Atlantic

Buccinum undatum [kidney] Solent, Hampshire, England. Material of F. R. Stranack.
Nucella lapillus [?] Dawlish, Devon, England (Sept., 1978). BM(NH) 1978.10.2.1.
Scrobicularia plana [kidney] Chalkwell, Essex, England. Material of J. Llewellyn.

(b) From elsewhere

Halichaeres bivittata [intestine] Bermuda (see Rees, 1970 : 205; as *Proctoeces subtenuis*). BM(NH) 1976.4.8.174.

(ii) NE Atlantic records from the literature

Buccinum undatum [kidney] Mellum Island, North Sea. Loos-Frank (1969 : 326; as *Proctoeces buccini*).
(?) —— [?] Scotland. Wootten, in White (1972 : 458; as *Proctoeces* sp.).
Scrobicularia plana [kidney] Chalkwell, Essex, England. Freeman & Llewellyn (1958 : 435; as *Proctoeces subtenuis*); Freeman (1962 : 199; 1963*a* : 113; 1963*b* : 253; as *P. subtenuis*); White (1972 : 458; as *P. subtenuis*).
—— [kidney] Whitstable, Kent, England. Freeman & Llewellyn (1958 : 435; as *Proctoeces subtenuis*).
—— [kidney] Dawlish Warren, Exe estuary, Devon, England. White (1972 : 458; as *Proctoeces subtenuis*).
—— [kidney] Estuaries of Rivers Jade and Wesef, Langwarden, West Germany. Loos-Frank (1969 : 329; as *Proctoeces scrobiculariae*).
—— [?] Burry Inlet, South Wales. James *et al*. (1977 : 13; as *Proctoeces subtenuis*).

ASPECTS OF BIOLOGY. The life-history and biology of this worm have been the object of a number of studies, and an interesting picture has emerged. It is apparent that in the warmer waters of its range, this species occurs as an adult in fishes. These fishes are normally shallow-water forms, principally labrids and sparids. This part of its range includes the shallow-waters of the Mediterranean and Black Seas, the southern North Atlantic, the eastern South Atlantic, the Caribbean

Sea, the Red Sea, New Zealand, Japanese and Hawaiian waters, the latter records indicating that it may occur widely in the shallow and warmer waters of the Pacific Ocean. There is a single report of *Proctoeces* in deep-water fishes by Kamegai (1974), who found them in *Peristedion orientale* and *Synchirops altivelis* off Japan. In the colder waters of its range in the northern hemisphere adults are found in molluscs. The degree to which the life-history is abbreviated varies. Sometimes the whole life-history apparently takes place in one host or, alternatively, adults sometimes occur in what appears to be a secondary molluscan host. Prevot (1965) and Lang & Dennis (1976), in pointing out that this so-called 'progenesis' appears to be more pronounced in temperate regions, have suggested that this may represent a mechanism to enable the species to extend into cooler waters without a dependence on its normal warm-water fish-hosts. Yet, it is apparent that several labrids and sparids are common around the British coast, and, although capable of being infested (Freeman, 1963*a*), there are no records in nature.

The daughter-sporocysts of this species have been found in the blood-vessels, blood-sinuses and digestive gland of *Mytilus* spp. Uzman (1953) described the cercariae shed by *Mytilus edulis* from the northeastern coast of the USA as *Cercaria milfordensis*, and simultaneously found ovigerous specimens of *Proctoeces* in the same host. Stunkard & Uzman (1959) found at least two sporocyst-generations, cercariae, metacercariae and ovigerous adults in this host, associating *Cercaria milfordensis* with *P. maculatus*, and postulated a telescoped or abbreviated life-history. The mother-sporocysts are globular and saccular, and each contain several daughter-sporocysts, which are simple, motile and orange. Evidently the sporocysts in the vascular system seriously reduce the efficiency of the circulatory system and destroy the gonads of the host, impair its vitality and are probably lethal. Dennis *et al.* (1974), however, found that the carbohydrate reserves and phosphatase activity of the mussel are not affected by the presence of *P. maculatus*. The cercaria is microcercous, but with a tendency to lose its tail, and possesses a 'Y'-shaped excretory vesicle. Although in some cases the entire life-history occurs in the one host, it is presumed that the mollusc is often ingested by a fish which becomes the final host. There may also be a transfer of cercariae from one mollusc to another. Lang & Dennis (1976) have summarized what is known of the seasonal incidence of *P. maculatus* in *Mytilus edulis* from the northeastern coast of the USA. Daughter-sporocysts evidently accumulate in the mussels and probably persist until the death of the host, whereas adult infestations in the kidney and pericardium of this host do not exhibit a cumulative pattern of intensity and apparently terminate annually with the death of the parasites.

Prevot (1965) discovered sporocysts of this species in *Mytilus galloprovincialis* in the Mediterranean. The second intermediate hosts he found were the polychaetes *Nereis caudata* and *Hydroides norvegica* and the molluscs *Patella coerulea* and *Acanthochites discrepens*. He was unable to find complete progenesis in *M. galloprovincialis* or *N. caudata*, many examples of which he examined, although some specimens did contain anomalous eggs. On being transferred to various fishes with a pipette, the parasites survived without maturation in *Gobius niger* and *Coris julis*, but matured in the labrid *Symphodus cinereus* [=*Crenilabrus griseus*]. Dupouy & Martinez (1973) similarly found the sporocysts in *M. galloprovincialis* and metacercariae in the polychaete *Leptonereis glauca*, and they stated that *P. maculatus* only rarely or indirectly 'castrated' this mussel.

The first intermediate host in north-eastern Atlantic waters is not known, unless *Cercaria tenuans* Cole, 1935, is a synonym of *C. milfordensis* Uzman, 1953, as tentatively suggested by Canzonier (1972). *C. tenuans* has been found in *Mytilus edulis* from Conway, North Wales and Boston, Lincolnshire, England (Coles, 1935), Padstow, Devon, England (Atkins, 1931), Ria de Arosa, northwestern coast of Spain (Canzonier, 1972) and Ria de Aveiro, Portugal (Dias & Serrano, 1972).

In our region unencysted adult specimens of *P. maculatus* occur in the kidney of the bivalve *Scrobicularia plana*. Its biology in this host has been studied by Freeman & Llewellyn (1958), Freeman (1962, 1963*a*, 1963*b*) and White (1972) from which the following data are taken. At Chalkwell in the Thames estuary every specimen of this bivalve examined was infested, and the total number of *S. plana* in the region numbered several million. The distribution, however, is restricted. It has been reported from Dawlish, Devon; but all of the specimens which we have examined from this region were uninfested. At Whitstable on the opposite bank of the Thames estuary from Chalkwell only three of many *S. plana* were found to be infested. In the severe winter of 1962–63 *S. plana* was eliminated from the part of the Thames estuary where it has been infested with *P. maculatus;* but on its return a build up of infestation was observed. Little seasonal variation occurs in the Thames estuary. Other bivalves in the Thames (e.g. *Mya* and *Macoma*) were not found to harbour *P. maculatus.* In *S. plana* an increase in the intensity of the infestation, up to a maximum of 14 per host, was found to be related to the size of the host. Parasites of varying sizes were found in the same host, so it would appear that there is no intraspecific inhibition to secondary infestations. In addition, many dead and 'petrified' worms were found in the kidneys of *S. plana.*

The environment in *S. plana* is osmotically variable, as the osmolarity of the host's body-fluids tends to follow that of the estuary. In this respect, therefore, the environment is more like that of a free-living estuarine turbellarian than a normal adult digenean. The trematode is red or pink due to the presence of a haem pigment but when the worm is in fishes this pigment declines in intensity. The haemoglobin was thought to have a respiratory function only when the oxygen tension is lowered as the valves close. Freeman (1963*b*) estimated that this oxygen store could last 25 minutes but Lee & Smith (1965) have corrected this figure to 2·5 minutes.

It has been suggested that *Proctoeces* is a recent addition to the British fauna and does not occur regularly in fish in this area, thus possibly explaining its apparent disjunctive distribution. With regard to its absence from fish-hosts, it should be pointed out, however, that there appears to be no evidence that labrid fishes which occur in the region of known foci of this parasite in *S. plana* have actually been examined. The only common labrid in the Thames estuary is *Symphodus* [=*Crenilabrus*] *melops*, which, although unlikely to feed on *S. plana*, is known to feed on *Mytilus edulis.* Attempts to infest the two labrids available in sufficient numbers at Plymouth, *Ctenolabrus rupestris* and *Symphodus melops*, have been made. Kidneys of *S. plana* from Chalkwell, where the incidence is 100%, were fed to the wrasses. Over half of these fishes were later found to be infested with *P. maculatus*; but the level of infestation decreased temporally. None were left after 6 days in *C. rupestris*; but on one occasion 5 specimens remained in *S. melops* for about 12–15 days. There were no significant morphological differences between the parasites from the invertebrate and the vertebrate hosts. The infestations in these wrasses were believed to be the result of being fed with the infested kidneys and it is possible that these parasites never survive for long in the fish-host.

'Progenetic metacercariae', or 'fully adult', *P. maculatus* have also been found in the gastropods *Buccinum undatum* (kidney) in the North Sea, *Nucella lapillus* in the English Channel (see above), *Gibbula umbilicalis* (intestine & radula) from Morocco (Dollfus, 1965, 1966), *Turbo cornutus* (kidney) from Japan (Ichihara, 1964, 1965) and *Rissoa splendida* (body-cavity) from the Black Sea (Dolgikh, 1965*b*, 1967). Loos-Frank (1969) believed that the whole life-history of this parasite could be completed in the whelk *Buccinum undatum.* Two further records, of unencysted non-ovigerous metacercariae of *Proctoeces*, may be the same species. These are those of Yamaguti (1938) from the liver of the bivalve *Brachidontes senhausi* and of Shimazu (1972) from between the epipodium and mantle of the gastropod *Haliotus discus hamai*. Both of the latter records are from Japan.

Timon-David (1934) described *Metacercaria psammechini* from the muscles of Aristotle's lantern, in the echinoderms (sea-urchins) *Psammechinus microtuberculatus* and *Sphaerechinus granularis* in the Mediterranean. He considered that it possibly belonged to *Proctoeces*, in the family Steringophoridae and pointed out that labrids commonly feed on echinoderms. In 1938, however, he stated that he was unsuccessful in his attempts at experimental 'contaminations', and his hypothetical attribution of these specimens to be Steringophoridae could not be maintained. Although certain superficial characteristics are reminiscent of *Proctoeces*, it appears that a number of features, notably the excretory system, may not conform to the fellodistomid pattern.

PREVIOUS DESCRIPTIONS. Looss (1901 : 402; as *Distomum maculatum*); Linton (1907 : 106; as *Distomum subtenue*); Odhner (1911 : 108); Vlasenko (1931 : 100); Yamaguti (1934 : 410); Manter (1947 : 321; as *Proctoeces erythraeus*; 1954 : 528; as *P. subtenue*); Hanson (1950 : 83;

figured); Koval, in Skrjabin & Koval (1957 : 394); Freeman & Llewellyn (1958 : 438; as *Proctoeces subtenuis*); Stunkard & Uzmann (1959 : 187); Manter & Pritchard (1962 : 115; figured); Freeman (1963*a* : 113; as *Proctoeces subtenuis*); Dollfus (1965 : 755; as *Proctoeces progeneticus*); Ichihara (1965 : 426; as *Proctoeces* sp.); Prevot (1965 : 178; figured); Dolgikh (1967 : 219); Naidenova (1967 : 487); Loos-Frank (1969 : 326; as *Proctoeces buccini*; 329; as *P. scrobiculariae*); Yamaguti (1970 : 39; as *Proctoeces hawaiiense*); Martinez (1974 : 39); Lang & Dennis (1976 : 66).

DESCRIPTION (Fig. 16). Six flattened whole-mounts were available for study. The subcylindrical worms taper at both ends and are widest at the level of the ventral sucker (Fig. 16a & b). The body-surface is smooth. The dimensions are included in Table 12. The subterminal *oral sucker* is smaller than the subglobular to oval *ventral sucker*, which is situated at about one-third of the body-length from the anterior end. There is a short prepharynx, a well-developed, globular *pharynx* and an oesophagus which is variable in length, normally being short or apparently absent. The intestinal bifurcation occurs in the mid-forebody, and the caeca, which are often dilate terminally, reach back to about half-way between the posterior testis and the posterior extremity of the body.

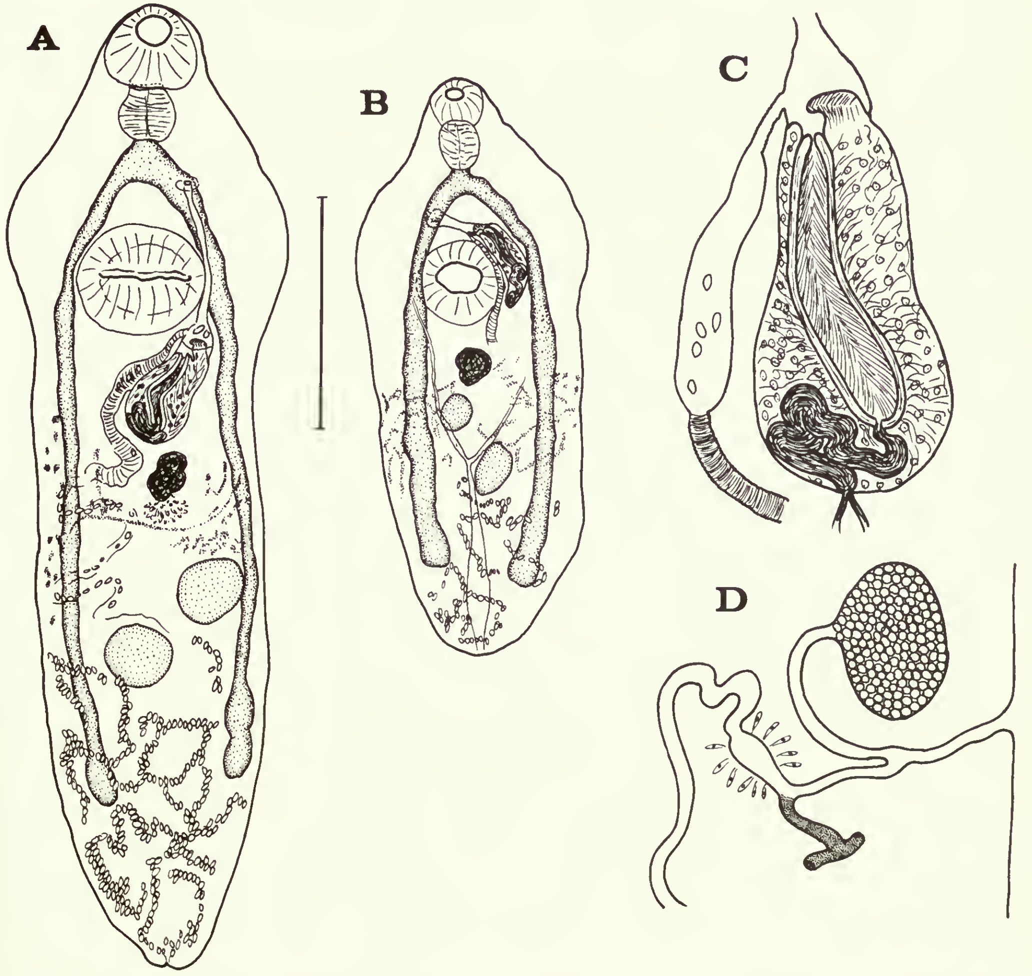


Fig. 16 *Proctoeces maculatus:* (a & b) flattened specimens – (a) ventral view of specimen from *Buccinum undatum:* (b) dorsal view of specimen from *Scrobicularia plana;* (c) cirrus–sac; (d) diagram of female proximal genitalia (modified after Freeman & Llewellyn, 1958). Bar scale: a, b = 1 mm.

Table 12 Dimensions of *Proctoeces maculatus* from the present material

Hosts	*Buccinum undatum*	*Scrobicularia plana*	*Halichaeres bivittata*	*Nucella lapillus*
Locality	Solent	Thames estuary	Bermuda	Devon
Length (mm)	2·3–4·4	2·6	1·46	1·7
Breadth (mm)	0·95–1·3	0·95–1·27	0·65	0·56
Length : forebody ratio	1 : 0·19–0·22	1 : 0·28	1 : 0·33	1 : 0·24
Oral sucker (mm)	0·27–0·36 × 0·30–0·44	0·23 × 0·23–0·24	0·20 × 0·28	0·17 × 0·18
Ventral sucker (mm)	0·40–0·54 × 0·49–0·64	0·35–0·37 × 0·42–0·43	0·33 × 0·40	0·30 × 0·38
Sucker-ratio	1 : 1·5–1·7	1 : 1·7–1·9	1 : 1·4	1 : 1·7
Pharynx (mm)	0·18–0·27 × 0·20–0·27	0·19–0·21 × 0·15–0·18	0·23 × 0·17	0·15 × 0·12
Oesophagus (mm)	0·00–0·09	0·02–0·04	0·05	0·04
Cirrus-sac (mm)	0·42–0·64 × 0·20–0·32	0·39–0·48 × 0·11–0·13	0·34–0·13	0·32–0·09
Testes (mm)	0·19–0·33 × 0·15–0·33	0·13–0·22 × 0·15–0·25	0·16–0·23 × 0·13–0·14	0·15–0·16 × 0·11–0·12
Ovary (mm)	0·19–0·23 × 0·14–0·24	0·13–0·17 × 0·14–0·18	–	0·13 × 0·13
Eggs (µm)	42–53 × 22–30	27–52 × 13–28	–	47–54 × 24–26

The terminal *excretory pore* opens into a 'Y'-shaped vesicle, which bifurcates at about the level of the testes. The arms reach anteriorly to about the level of the pharynx.

The globular or subglobular *testes* lie in tandem to obliquely in the middle of the hindbody. The vasa efferentia pass forward, uniting almost immediately before they pass through the wall of the *cirrus-sac*. The latter organ, which is elongate-oval to claviform varies in position from being entirely in the hindbody, to partly in the forebody (Fig. 16a & b), but usually lies postero-dorsal, postero-lateral, dorsal or antero-dorsal to the ventral sucker. Its actual position depends upon the degree of contraction of the genital atrium. The cirrus-sac contains the entire seminal vesicle, the pars prostatica and the ejaculatory duct (Fig. 16c). The small, tubular seminal vesicle is coiled at the proximal extremity of the cirrus-sac. The well-developed, wide pars prostatica fills much of the cirrus-sac, sometimes extending to its proximal extremity. It is almost straight to arcuate, and possesses a filamentous lining and a dense covering of gland-cells that fill much of the space remaining in the cirrus-sac. The ejaculatory duct is short, muscular and capable of being everted to form a small, conical cirrus. Beside the opening of the male duct, or the cirrus, is a prominent muscular papilla. The cirrus and associated papilla may be extruded through the genital pore in certain specimens. The genital atrium is variable in length, but is usually long (deep) and narrow (Figs 16a & b). The genital pore lies ventrally to the left of the median line at about the level of the intestinal bifurcation.

The *ovary* is globular or slightly lobed, and is usually slightly smaller than the testes. It lies anteriorly to the testes, more or less in the median line. The oviduct leaves the ovary mid-ventrally and passes posteriorly, receiving Laurer's canal, and then ventrally, receiving the common vitelline duct, before entering an inconspicuous Mehlis' gland and dilating to form a distinct oötype. Laurer's canal is short, simple and opens mid-dorsally at the level of the region between the ovary and the anterior testis (Fig. 16d). There is no seminal receptacle, and although no uterine seminal receptacle has been reported or is visible in the flattened whole-mounts which we have examined, we suggest that, in the absence of any other seminal storage mechanism, one may be present. The *uterus* is variable in size, usually extending throughout the hindbody, occasionally filling it, or sometimes consisting of only a small number of loops. It initially loops posteriorly towards the posterior extremity, whereupon it passes forward to about the level of the ovary, where it forms a distinct, muscular metraterm. The latter duct passes anteriorly more or less directly and enters the base of the genital atrium. The uterine coils, which reach extra-caecally, occur mainly posterior to the testes, lateral to the testes, and to a lesser extent between the ovary and the ventral sucker. The uterus contains numerous operculate eggs with unmodified shells. The *vitellarium* is irregularly follicular, the follicles exhibiting different degrees of development. The follicles occur in two symmetrical, lateral fields, the normal limits of distribution of which are the levels of the anterior margin of the ovary and the posterior margin of the hind testis, but they occasionally overreach these limits. Alternatively, the vitellarium may be greatly reduced or difficult to distinguish, and apparently consist of only a few scattered globular or elongate follicles (Figs 16a & b). The main transverse vitelline collecting ducts, when visible, unite postero-ventrally to the ovary and form a short common vitelline duct. The latter may swell, forming a small vitelline reservoir.

DISCUSSION. Looss (1901) originally described this species, as *Distomum maculatum*, from the labrids *Labrus merula*, *Thalassoma* [=*Crenilabrus*] *pavo* and *Symphodus cinereus* [=*Crenilabrus griseus*] in the Adriatic Sea at Trieste. Linton (1907) then described a similar worm as *Distomum subtenue* from the sparid *Calamus calamus* and the labrids *Bodianus rufus* [=*Harpe rufa*], *Halichaeres* [=*Iridio*] *bivattata* and *Lachnolaimus maximus* from off Bermuda. It was not differentiated from *D. maculatum*, but the egg-measurement given is rather smaller. Further studies, however, have shown egg-size to be a particularly unreliable criterion for this species, and no further convincing evidence has been produced to uphold the validity of *D. subtenue* as a distinct species.

In 1911 Odhner erected the genus *Proctoeces* for *D. maculatum* and a new species, *P. erythraeus*, from *Sparus* [=*Chrysophrys*] *bifasciata* and *Thalassoma* [=*Iulus*] *lunare* in the Red Sea. Subsequent studies (Hanson, 1950; Freeman & Llewellyn, 1958) have shown that *P. erythraeus*, which was originally distinguished on egg-size, sucker-size and vitelline configuration, falls well within the known morphological range of *P. maculatus*. Recent workers (Manter & Pritchard, 1962; Overstreet, 1969; Lang & Dennis, 1976) have considered both *P. subtenuis* and *P. erythraeus* as synonyms of *P. maculatus*.

Proctoeces major Yamaguti, 1934, was originally described from *Pagrosomus auratus* off Japan. It was said to differ from *P. maculatus* in having a distinctly trilobed ovary. Although in some fellodistomid groups the ovary appears to be constant, in others it varies considerably. Despite the fact that the ovary of *P. maculatus* is usually described as globular, occasional specimens of this species with a trilobed ovary have been found (Vlasenko, 1931; Freeman, 1963*b*; Dollfus, 1965). Dolgikh (1967) figured a specimen which she called '*P. major* (?)' that was found in her collection of *P. maculatus* from the gastropod *Rissoa splendida* in the Black Sea. Ichihara (1965) described *Proctoeces* sp. from the gastropod *Turbo cornutus* in Japan as having 54% of the specimens with trilobed ovaries and 46% with globular ovaries. Ichihara's specimens are herein considered to be *P. maculatus*. We tentatively include *P. major* as a synonym of this species; but we note certain morphological similarities between Yamaguti's (1934) description of *P. major* and *Xenopera insolita* Nicoll, 1915. The posterior limit of the caeca is closer to the posterior extremity than is apparent in the descriptions of *P. maculatus*, and there is a hint of an external seminal vesicle in Yamaguti's figure (1934, fig. 79).

Dollfus (1965) described *P. progeneticus* from *Gibbula umbilicalis* in Morocco. The differentiating features that he invoked are not convincing, and his specimens fit into the known variation described by Freeman & Llewellyn (1958). Dollfus' figures 2 and 3 illustrate the condition of the worm when the copulatory organ is extruded through the genital pore. The variations described by Freeman & Llewellyn also encompass the specimens described as *P. buccini* and *P. scrobiculariae* by Loos-Frank (1969). Lang & Dennis (1976) discuss the validity of *P. scrobiculariae*, giving their reasons for considering it a synonym of *P. maculatus*. In 1970 Yamaguti described *P. hawaiiense* from *Monotaxis* sp. (? *grandoculis*) off Hawaii. He differentiated it from *P. lintoni* Siddiqi & Cable, 1960, but not from *P. maculatus*, and his three specimens do not appear to be distinguishable from the latter, especially from the specimen from Hawaii figured by Manter & Pritchard (1962).

In synonymizing all of these species with *P. maculatus*, we are accepting that it must be a variable species occurring in widely dissimilar hosts. Perhaps its variability is the result of a wide host-tolerance; but both Freeman & Llewellyn (1958) and Stunkard & Uzman (1959) found a high level of variation in specimens from *Scrobicularia plana* and *Mytilus edulis*, respectively.

Subfamily **MONASCINAE** Dollfus, 1947

Haplocladinae Odhner, 1911.

DIAGNOSTIC FEATURES. Body small to medium-sized; elongate; sub-cylindrical. Body-surface smooth. Oral sucker more or less terminal; slightly larger than ventral sucker. Ventral sucker inside anterior third to quarter of body. Prepharynx absent. Pharynx elongate. Caecum single; short anterior region (? oesophagus) with tegumental lining; long posterior region with epithelial lining (? opens into excretory vesicle close to posterior extremity forming uroproct.) Testes two; tandem; usually separated by part of uterus; in posterior half of hindbody; usually sinistral. Cirrus-sac broadly oval; normally antero-sinistral or partly dorso-sinistral to ventral sucker. Seminal vesicle bipartite; internal. Pars prostatica well developed; tubular; wide; curved; with filamentous lining and many external gland-cells. Ejaculatory duct wide; muscular; diverticulate. Spermatophores occasionally seen. Genital atrium small. Genital pore sinistrally submedian; ventral in posterior half of forebody. Ovary entire to trilobed; pre-testicular; separated from anterior testis by part of uterus; sinistral in about middle of body. Mehlis' gland pre-ovarian. Laurer's canal and uterine seminal receptacle present. Uterine coils fill much of hindbody, reaching to posterior extremity; open into base of genital atrium. Eggs numerous; small; operculate. Vitellarium follicular; in two symmetrical, lateral fields; between levels of ventral sucker and testes. Excretory vesicle 'Y'-shaped; bifurcation just posterior to ovary; arms reaching to level of pharynx or oral sucker. Parasitic in intestine of marine teleosts (predominantly Perciformes).

COMMENT. This subfamily contains only one genus, i.e. *Monascus* Looss, 1907, as *Haplocladus* Odhner, 1911, is clearly a synonym (see below). Travassos *et al.* (1965) raised the Monascinae to full family-status; but there are a number of features, such as the basic anatomy of the reproductive and excretory systems, which indicate that it is closely related to other fellodistomid groups. In particular, the contents of the cirrus-sac and the formation of spermatophores suggest this affinity.

Genus ***MONASCUS*** Looss, 1907

Haplocladus Odhner, 1911.

DIAGNOSTIC FEATURES. As family.

TYPE SPECIES. *Monascus filiformis* (Rudolphi, 1819) (by original designation).

COMMENT. We consider this genus to be monotypic (see below).

Monascus filiformis (Rudolphi, 1819) Looss, 1907

Distoma filiforme Rudolphi, 1819.
Haplocladus filiformis (Rudolphi) Odhner, 1911.
Haplocladus typicus Odhner, 1911.
*Monascus typicus** (Odhner) Dollfus, 1947.
Haplocladus minor Odhner, 1911.
Monascus minor (Odhner) Dollfus, 1947.
Haplocladus orientalis Srivastava, 1937.

---

* *Monascus monenteron* Looss, 1907 *nomen nudum*, has been considered (e.g. Looss, 1912; Fischthal & Kuntz, 1963) a synonym of *M. typicus*.

Monascus orientalis (Srivastava) Yamaguti, 1958.
Monascus netoi Travassos, Teixeira de Freitas & Bührnheim, 1965.
Monascus chauhani Kumari, 1975.
Monascus ovilobatus Kumari, 1975†.
Monascus elongatus Karyakarte & Yadav, 1976.

TYPE-HOST AND LOCALITY. *Cepola rubescens*, Rimini, Italy.

RECORDS
(i) Material studied
(a) From the NE Atlantic
Limanda limanda [intestine] Tjarno, Sweden (Aug., 1972). Material of J. Thulin.
—— [?] Carmarthen Bay, Dyfed, Wales (Sept.–Nov., 1976). Collected by H. Al-Abdul-Jabbar. BM(NH) 1977.6.29.1–4.
Trachurus trachurus [intestine] Plymouth, Devon, England (April, 1937) (see Rees [W. J.], 1947 : 604) BM(NH) 1970.1.12.13 (May, 1972) BM(NH) 1977.6.29.5–7.
—— [intestine] Vinga, west coast of Norway (Oct., 1973). Material of J. Thulin.

(b) From elsewhere
Trachurus lathami [body-cavity] El Dique, Cumana, Sucre State, Venezuela (see Nasir & Gomez, 1977 : 70) BM(NH) 1976.3.19.8.

(ii) NE Atlantic records from the literature
(a) Mature
Limanda limanda [intestine] Kristineberg, Sweden (1898). Odhner (1911*a* : 105; as *Haplocladus minor*).
—— [intestine] Western Kattegat. Køie (1979 : 117).
Trachurus trachurus [intestine] Plymouth, Devon, England. Rees (1947 : 604; as *Haplocladus typicus*).
—— [intestine] Strait of Gibraltar. Kovaleva (1969 : 132; 1970*a* : 53; as *Haplocladus typicus*).
—— [intestine] Western Kattegat. Køie (1979: 117).

(b) Immature
Arnoglossus laterna [intestine] Western Kattegat. Køie (1979: 117).
Buglossidium luteum [intestine] Western Kattegat. Køie (1979: 117).
Crystallogobius linearis [intestine] Western Kattegat. Køie (1979: 117).
Glyptocephalus cynoglossus [intestine] Western Kattegat. Køie (1979: 117).
Pomatoschistus minutus [intestine] Western Kattegat. Køie (1979: 117).

ASPECTS OF BIOLOGY. Larval stages of *Monascus filiformis* recorded in the NE Atlantic.
Nucula nitidosa [?] Western Kattegat. Køie (1979: 114).
Nucula nucleus [digestive gland and gonads] Cawsand Bay, Plymouth Sound, Devon, England. Rees (1947 : 602; as *Haplocladus* sp.). BM(NH) 1970.1.12.14.
Nucula nucleus or *Abra* [=*Syndosmya*] *alba* [cercariae free in aquarium] Kristineberg, Sweden. Odhner (1911*a* : 105; as *Haplocladus minor*).

Rees (1947) described the cercaria, two to ten of which he found in each infested specimen of the bivalve *Nucula nucleus*. The cercariae arise from daughter-sporocysts, which, according to our observations on one of his specimens, may have a terminal birth-pore. Each cercaria is large, up to about 3 mm in length, including the long, bifurcate tail, the furcae of which are variable in size. A long caecum which does not appear to unite with the excretory vesicle and a short diverticulum were observed. Køie (1979) also described the cercaria. She found that *Limanda limanda* became infested by eating cercariae, and *Trachurus trachurus* became infested by feeding on *Crystallogobius linearis*, which eats cercariae, but in which the worm does not mature. It would appear that sperm-transfer involves spermatophores, as these have been reported by Odhner (1911*a*) and Fischthal & Kuntz (1963).

---

† *Monascus chauhani* is the name given by Kumari (1975) at the head of the description, but the figure is labelled *M. ovilobatus*.

The adult worms occur mainly in carangids, although a wide range of other fish are also infested (see below). The species has a widespread distribution, including not only the northeast Atlantic and both the Mediterranean and Black Seas, but also the Gulf of Mexico, the Atlantic coast of South America and Africa, the Pacific coast of Central America and the coastal regions of India and the Arabian peninsula.

PREVIOUS DESCRIPTIONS. Odhner (1911*a* : 104; as *Haplocladus typicus* and *H. filiformis*; 105; as *H. minor*); Vlasenko (1931 : 99; as *Haplocladus typicus*); Srivastava (1941 : 42; as *Haplocladus orientalis*); Dollfus (1947 : 319); Janiszewska (1953 : 41; as *Haplocladus typicus*); Koval, in Skrjabin & Koval (1957 : 358; as *Haplocladus typicus*); Fischthal & Kuntz (1963 : 177; as *Monascus typicus*); Nikolaeva (1963 : 413; as *Haplocladus typicus*); Travassos *et al*. (1965 : 46; 1967 : 25; as *Monascus netoi*); Lamothe-Argumedo (1969 : 179; as *Monascus typicus*); Hafeezullah & Siddiqi (1970 : 934, figure only; as *Monascus typicus*); Nahhas & Powell (1971 : 2); Fischthal & Thomas (1972*b* : 297; as *Monascus typicus*); Kumari (1975 : 248; as *Monascus chauhani* and *M. ovilobatus*); Karyakarte & Yadav (1976 : 169 as *M. elongatus*; 172 as *M. typicus*); Nasir & Gomez (1977: 70); Køie (1979: 123).

DESCRIPTION (Fig. 17). This account is based upon 15 specimens, three of which were serially sectioned. The dimensions of the worms are given in Table 13, but these preserved specimens studied were either flattened or poorly fixed. The body of these small to medium-sized worms is elongate and sub-cylindrical, possessing a smooth tegument. The body-wall contains prominent diagonal muscles. The *oral sucker* is sub-globular to slightly elongate, opens more or less terminally and may be slightly withdrawn (Fig. 17b). It is usually slightly larger than the circular *ventral sucker*, which lies in the anterior third (usually quarter) of the body. There is no prepharynx, as the oral sucker abuts directly onto an elongate and large *pharynx*, which leads into an oesophagus and a single caecum. The oesophagus is short, slightly narrower than the caecum and possesses a tegumental lining: the latter clearly distinguishes it from the caecum, which is lined by cuboidal epithelium. The caecum tends to be dorso-dextral and at the posterior end of the body, it apparently narrows to a short duct which may form a uroproct. Køie (in litt.) was unable to find a uroproct and our material is unclear in this respect. In a sectioned specimen a short caecal diverticulum was seen between the ventral sucker and the ovary, this is probably the 'reduced left caecum' of Koie (1979).

The terminal *excretory pore* leads into a narrow, 'Y'-shaped vesicle, which passes ventrally to the caecum and usually bifurcates posteriorly to the level of the ovary in fully-developed worms, although in one of our sectioned specimens the bifurcation was just anterior to the ovary. The arms reach forward into the forebody to the level of the pharynx.

The rounded *testes* lie in tandem in the hindbody. In small worms they lie close together and close to the posterior extremity; but, as the uterus grows, it appears to force them further apart and also forms a large number of coils in the post-testicular region, where the hindbody extends in order to accommodate it. This form of allometric growth has caused some confusion in the taxonomy of this genus. The testes normally lie towards the left side of the body. The vasa efferentia were not visible in our sections; but, according to Fischthal & Kuntz (1963), they unite almost immediately prior to passing through the wall of the cirrus-sac, forming a short vas deferens. The *cirrus-sac* is globular to oval, large and situated antero-sinistral to the ventral sucker, although it may be antero-dorsal in unflattened specimens. Within the cirrus-sac there is a bipartite seminal vesicle, the parts of which tend to be oval to globular, the pars prostatica and the ejaculatory duct (Fig. 17a). The seminal vesicle is small and lies in the proximal region of the cirrus-sac. The pars prostatica is tubular, wide and curved, possessing a filamentous lining and a dense external covering of gland-cells that fill much of the available space within the cirrus-sac. The ejaculatory duct is short, wide and diverticulate, and although not seen in our material, it may evert to form a conical cirrus which may protrude through the genital pore (see fig. 2 of Fischthal & Kuntz, 1963). No spermatophores were seen associated with the terminal

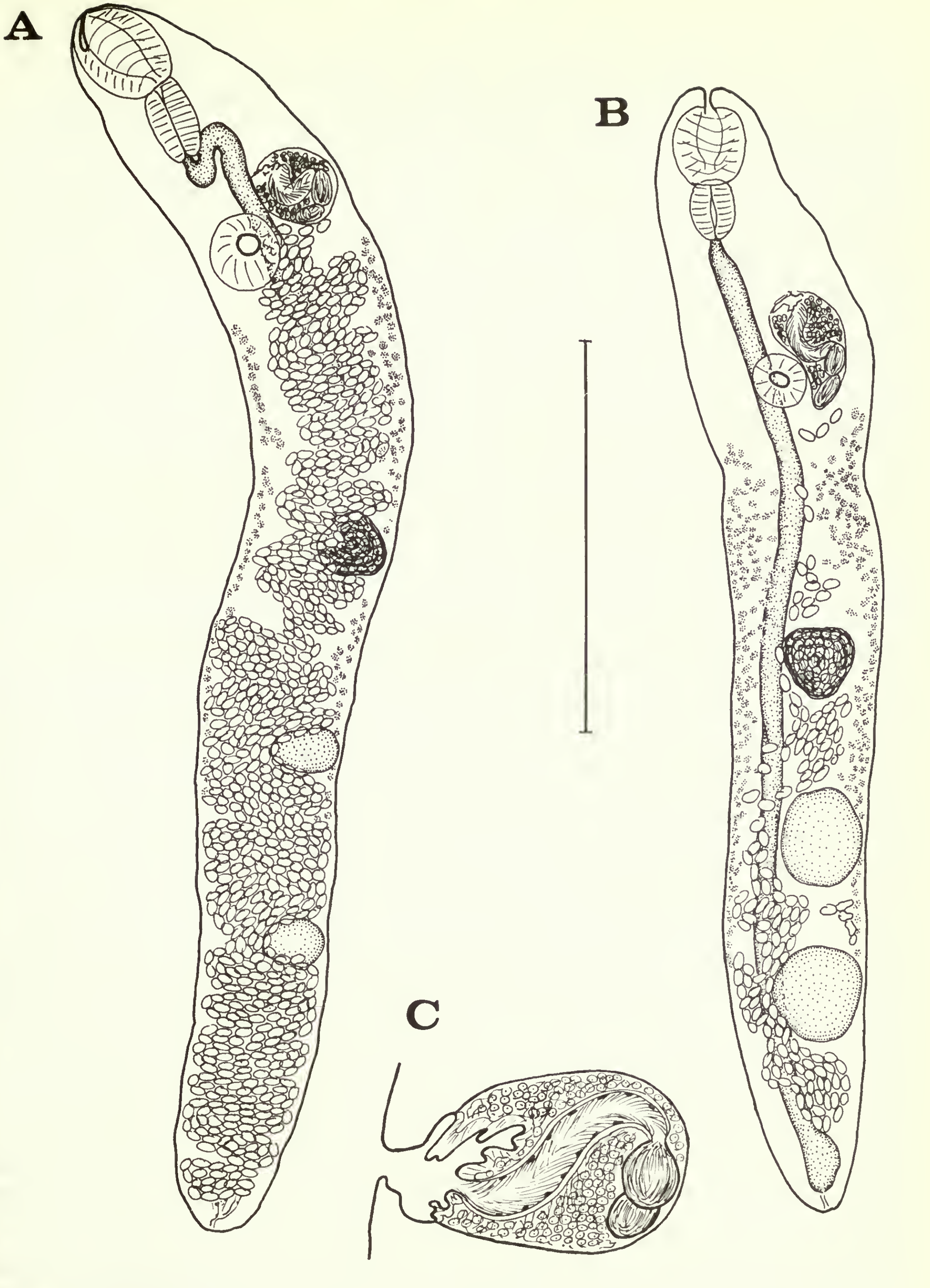


Fig. 17 *Monascus filiformis:* (a) specimen from *Trachurus trachurus:* (b) specimen from *Limanda limanda*; (c) cirrus-sac. Bar scale: a, b = 1 mm.

Table 13 Dimensions of *Monascus filiformis* from the present material and from the literature

Authority	Nasir & Gomez (1977)	Present material	Present material
Name used	*Monascus filiformis*	*Monascus filiformis*	*Monascus filiformis*
Hosts	*Trachurus lathami*	*Limanda limanda*	*Trachurus trachurus*
Locality	Venezuela	see text	see text
Length (mm)	4·3–4·9	2·8–5·3	1·3–7·6
Breadth (mm)	0·26–0·43	0·48–0·67	0·23–0·52
Length : forebody ratio	1 : 0·20	1 : 0·15–0·23	1 : 0·22–0·33
Oral sucker (mm)	0·21–0·25 × 0·13–0·19	0·21–0·35 × 0·19–0·27	0·16–0·17 × 0·13–0·22
Ventral sucker (mm)	0·13–0·23 dia.	0·14–0·25 × 0·14–0·26	0·11–0·21 × 0·11–0·21
Sucker-ratio	1 : 1	1 : 0·74–0·95	1 : 0·80–0·95
Pharynx (mm)	0·15–0·21 × 0·10–0·135	0·16–0·28 × 0·11–0·15	0·09–0·15 × 0·15–0·20
Oesophagus (mm)	–	0·045	0·02–0·14
Cirrus-sac (mm)	0·25–0·51 × 0·10–0·33	0·32 × 0·17–0·21	0·14–0·38 × 0·08–0·20
Testes (mm)	0·17–0·28 dia.	0·21–0·29 × 0·23–0·29	0·06–0·26 × 0·08–0·26
Ovary (mm)	0·17–0·21 dia.	0·18–0·20 dia.	0·07–0·23 × 0·10–0·21
Eggs (μm)	26–28 × 16–18 (our data: 34–36 × 21–25)	40–49 × 22–28	40–46 × 22–31

genitalia of our material; but their occurrence in this species has been reported (see above). The genital atrium is small and opens via the genital pore ventrally on the left side of the posterior half of the forebody.

The *ovary* varies in shape from being more or less globular to being trilobed. It lies directly anterior to the testes in small worms, but becomes separated from the anterior testis by coils of the uterus as the worm grows. In fully grown worms it is normally in about the middle of the body, but slightly towards the left side. The exact details of the remainder of the proximal region of the female reproductive system are difficult to make out in our material, and other workers do not appear to have described this region in detail. It appears, however, that the oviduct arises ventrally, passes anteriorly and is almost immediately united with Laurer's canal which opens dorsally. The oviduct then passes over the anterior surface of the ovary and receives the common vitelline duct as it passes into an indistinct Mehlis' gland situated anteriorly to the ovary. There is a small uterine seminal receptacle present. The *uterus* fills most of the hindbody, especially in the ventral field, reaching to or close to the posterior extremity, but not passing to the left of the gonads. It appears to form a simple, narrow metraterm at about the level of the ventral sucker, and this passes directly forward sinistrally or ventro-sinistrally to the cirrus-sac and enters the base of the genital atrium. The uterus contains numerous operculate eggs with smooth shells. The *vitellarium* consists of numerous small follicles in two symmetrical, lateral fields between the level of the ventral sucker and the level of the testes. The exact limits are, however, variable: the anterior limit may be just posterior to the ventral sucker, while the posterior limit varies between the anterior margin of either testis. The transverse vitelline ducts unite anteriorly to the ovary to form the common duct, which is swollen to form a small vitelline reservoir.

DISCUSSION. The genus *Monascus* was erected by Looss (1907) for *Distoma filiforme* Rudolphi, 1819, the type-species, and *M. monenteron* nom. nud. Without reference to this work Odhner (1911*a*) erected the genus *Haplocladus* for *H. typicus*, type-species, and two other species, one of which was *H. filiformis* (Rudolphi, 1819). In 1912 Looss indicated that *Monascus filiformis* and *Haplocladus filiformis* were synonymous [although erroneously referring to Rudolphi's material as *Distoma filicolle* instead of *D. filiforme*], and that *H. typicus* of Odhner was identical to his own *M. monenteron*. As Looss's comments were made in a footnote, it was not until the work of Dollfus (1947) that *Haplocladus* was generally recognized as being a synonym of *Monascus*.

We believe that all of the described species of this genus can be considered synonymous, as attempts to separate them have been unconvincing. It is evident that the continued recognition of some of the species was based, at one time, solely on the host-species. The early records of *M. filiformis* were from *Cepola rubescens*, *M. typicus* was recorded in *Trachurus trachurus* and *M. orientalis* (Srivastava, 1937) in *Synaptura orientalis*. The hosts of other species, each recorded only once , are: *M. minor* (Odhner, 1911) in *Limanda limanda; M. netoi* Travassos *et al*., 1965, in *Oligoplites saurus*; *M. chauhani* Kumari, 1975, in *Pampus* spp. and *M. elongatus* Karyakarte & Yadav, 1976 in *Stromateus niger*. As further records of *M. filiformis*, *M. typicus* and *M. orientalis* accumulated a greater variety of hosts were recorded. The additional hosts of these species are:

M. filiformis –	Carangidae	– *Trachurus lathami* (Nasir & Gomez, 1977) *Decapterus punctatus* (Nahhas & Powell, 1971)
M. orientalis –	Nemipteridae	– *Nemipterus japonicus* (Parukhin, 1973, 1976)
	Serranidae	– *Epinephelus ascolatus* (Parukhin, 1976)
M. typicus	– Carangidae	– *Trachurus mediterraneus* (Janiszewska, 1953; Nikolaeva & Kovaleva, 1966; Kovaleva, 1969, 1970*a*) *T. mediterraneus ponticus* (Nikolaeva, 1963; Nikolaeva & Kovaleva, 1966; Kovaleva, 1965, 1968, 1969, 1970*a*, 1970*b*) *T. trecae* (Kovaleva, 1975) *T. picturatus* (Kovaleva, 1975) *Decapterus russelli* (Fischthal & Kuntz, 1963; Hafeezullah & Siddiqi, 1970; Parukhin, 1976) *D. rhonchus* (Fischthal & Thomas, 1968) *Selar* [=*Trachurops*] *crumenophthalmus* (Fischthal & Thomas, 1968, 1972*b*; Lamothe-Argumedo, 1969; Parukhin, 1970, 1976). *Caranx hippos* (Lamothe-Argumedo, 1969; Papoutsoglou, 1976). *C. armatus* and *C.* sp. (Parukhin, 1976). *Chloroscombrus chrysurus* (Fischthal & Thomas, 1968).
	– Cepolidae	– *Cepola rubescens* (Sey, 1970)
	– Lethrinidae	– *Lethrinus miniatus* (Parukhin, 1976).
	– Stromateidae	– *Pampus argenteus* (Madhavi, 1975) *Stromateus maculatus* (Gaevskaja & Kovaleva, 1978)
	– Clupeidae	– *Sardinella aurita* (Parukhin, 1970, 1975, 1976).
	– Scombridae	– *Scomber colias* (Eremina, 1970)
	– Balistidae	– *Abalistes stellatus* (Parukhin, 1978)
	– Platycephalidae	– *Platycephalus macrocanthus* (Karyakarte & Yadav, 1976)
	– Characidae	– *Hydrocynus forskalii* (Fischthal & Kuntz, 1963).

As far as the relationships of these fishes are concerned (see Nelson, 1976), there seems to be no basis for the separation of *Monascus* on the grounds of host-group specificity. While it appears that the majority of hosts belong to the family Carangidae (*Caranx*, *Trachurus*, *Oligoplites*, *Decapterus*, *Selar*, *Chloroscombrus*), other closely related and even quite different fishes may become infested. The most closely related to the carangids are *Cepola* (Cepolidae), *Lethrinus* (Lethrinidae), *Epinephelus* (Serranidae) and *Nemipterus* (Nemipteridae), as these all belong to the suborder Percoidei, and *Stromateus* and *Pampus* (Stromateidae; not a flatfish, as referred to by Kumari, 1975) and *Scomber* (Scombridae) belong to the same order, the Perciformes. Unrelated forms belong to the Clupeiformes (*Sardinella*), Pleuronectiformes (*Limanda*, *Synaptura*), Scorpaeniformes (*Platycephalus*), Tetraodontiformes (*Abalistes*) and the essentially freshwater Cypriniformes (*Hydrocynus*).

The morphological features which have been used to distinguish the above species are mostly trivial and can be dismissed. Odhner (1911*a*) distinguishes *M. typicus* and *M. filiformis* on egg-size and colour and the position of the testes in the hindbody. As pointed out by Fischthal & Kuntz (1963) and as shown in Table 13, egg-size apparently varies considerably, and is even inconsistent amongst specimens from the same host-species. The colour of the eggs is probably a function of the degree of tanning which has taken place and, as is seen in many other fellodistomids, the degree of tanning may be correlated to the size of the eggs, which normally get smaller as the tanning becomes more intense. Skrjabin & Koval (1957) also use the position of the testes in the hindbody, in addition to the dimensions of the oral sucker, the length of the body and the posterior limit of the vitellarium, to separate *M. typicus*, *M. orientalis*, *M. minor* and *M. filiformis*. The hindbody, however is known to extend during development, becoming much longer relative to the forebody, the post-testicular region also develops allometrically and the testes separate (Dollfus, 1947; Fischthal & Thomas, 1972*b*). The size of the oral sucker and overall length are subject to great variation merely due to the growth of the worm, and the vitellarium is variable, particularly with regard to its posterior limit. Fischthal & Thomas (1968) could find no difference between *M. filiformis* and *M. typicus*, but stated that a 'final decision' on synonymy must await life-history studies. As all taxonomic criteria in this group are based upon comparative morphology, there seems to be no satisfactory basis for considering that these two species are distinct.

M. orientalis is said to differ from *M. typicus* in 'size ratio of suckers, size of various organs, extent and character of vitellaria and the topography of the gonads' (Srivastava, 1937) and the 'cephalad position of the acetabulum' (Srivastava, 1941). References to Table 13 and to Srivastava's (1941) figure suggests that these characters are more or less typical of those in *M. filiformis*. The only character which might be significant is the reported spinous nature of the tegument, but this is questionable and requires confirmation.

M. netoi is considered by Travassos *et al.* (1965) to differ from other species of *Monascus* in having a pharynx longer than the oral sucker. As they had only a single specimen there is no indication of the variation in this feature; but it is not at all dissimilar to that of *M. filiformis* as illustrated by Dollfus (1947). *M. chauhani*, according to Kumari (1975), differs from all known species of the genus in the larger size of the body, the oral sucker having a slit-like opening and the distinctly lobed ovary. However, it is not significantly larger than other records of *Monascus*, the slit-like opening of the oral sucker is probably a fixation-artifact and is known to occur in *M. filiformis* (see Fig. 17a), and the trilobation of the ovary appears to be fairly typical of some specimens of *M. filiformis*, where a range of form from virtually globular to distinctly trilobed occurs. When Madhavi (1975) found specimens of *Monascus* in *Pampus*, the same genus of host as *M. chauhani* and also off the Indian coast, he referred to them as *M. typicus*. *M. elongatus* is similar to *M. chauhani* and is here considered synonymous with *M. filiformis* for the same reasons.

Subfamily **TERGESTIINAE** Skrjabin & Koval, 1957

DIAGNOSTIC FEATURES. Body small to medium-sized; elongate; cylindrical. Most of body-surface smooth; but oral sucker normally surrounded by ring of about 13–20 muscular cephalic lobes, interrupted ventrally; 'neck'-region normally with six muscular flanges ('collarettes') on each lateral surface at about level of pharynx. Oral sucker subterminal to terminal; usually larger than ventral sucker, but may be of similar size or smaller. Globular ventral sucker in anterior half of body. Prepharynx absent. Pharynx normally well developed; elongate. Oesophagus well developed often long. Intestinal bifurcation in forebody or anterior hindbody. Caeca long, reaching close to posterior extremity; blind. Testes two; oval or irregularly oval; tandem to oblique; in posterior half of hindbody. Cirrus-sac normally bipartite; usually extending back dorsally and posteriorly to ventral sucker; posterior part elongate, normally contains seminal vesicle; anterior part globular, normally contains pars prostatica and ejaculatory duct. Seminal vesicle elongate; saccular. Pars prostatica small; vesicular; with indistinct lining. Ejaculatory duct large; muscular; complex; deeply diverticulate; may be completely everted through genital pore to form large, lobed cirrus. Genital atrium deep. Genital pore median to sinistrally submedian; ventral in posterior forebody. Ovary reniform to oval; pre-testicular; somewhat near middle of hindbody. Mehlis' gland dorsal to ovary. Laurer's canal and uterine seminal receptacle present. Uterine coils extend from ventral sucker back to posterior extremity or to level of testes; uterus opens into base of genital atrium via muscular metraterm. Eggs numerous; small; operculate. Vitellarium follicular; in two symmetrical, lateral fields in hindbody; fields may be confluent. Excretory vesicle 'Y'-shaped; bifurcation in about mid-hindbody; arms reaching to level of pharynx. Parasitic in intestine (often rectum) of marine teleosts.

COMMENT. We accept three genera in our conception of this subfamily. These are *Tergestia* Stossich, 1899, *Theledera* Linton, 1910, and *Gymnotergestia* Nahhas & Cable, 1964. In his revision of the genus *Tergestia*, Dollfus (1973) accepted *Theledera* as a subgenus of *Tergestia* on the basis of the difference in the position of the intestinal bifurcation, although earlier workers (Manter, 1940; Siddiqi & Cable, 1960) had synonymized the two genera. From Dollfus' work, it appears, however, that the material of Siddiqi & Cable and that of Manter, described later (1947), are specimens of *Tergestia* and not *Theledera*. We accept *Theledera* as a valid genus because of the distinct differences in the position of the intestinal bifurcation, it being in the forebody in *Theledera* and either postero-dorsal to the ventral sucker or clearly in the hindbody in *Tergestia*. We also note that in *Theledera* there is a tendency for the uterus not to reach beyond the testes, whereas in *Tergestia*, in mature specimens, it usually reaches posteriorly to the testes: there are, however, several exceptions to this. We note that there appear to be certain differences in the shape of the cirrus-sac in the species described in the literature. We consider, however, that the normal situation is that the cirrus-sac is bipartite and that the seminal vesicle occupies much of the posterior part. Examples of such variations on this pattern include *Tergestia kuhliae*, described by Yamaguti (1970), where the pars prostatica apparently occurs in the posterior part of the cirrus-sac and *Gymnotergestia chaetodipteri*, described by Nahhas & Cable (1964), where the cirrus-sac does not appear to be bipartite, although one of the figures does suggest a slight constriction. In some descriptions the exact shape of the cirrus-sac was not clearly indicated. *Gymnotergestia* differs from both *Tergestia* and *Theledera* in lacking the elaborate muscular ornamentation on the forebody and around the oral sucker: this is replaced by superficial tegumental annulations in the anterior forebody. It also differs from *Tergestia* in having the intestinal bifurcation in the forebody and apparently from both genera, as mentioned above, in having a less distinctly bipartite cirrus-sac. Only *Tergestia* occurs in the northeast Atlantic region.

While *Gymnotergestia* is monotypic, *Theledera*, of which *Cithara* MacCallum, 1917, and *Tergestina* Nagaty & Abdel Aal, 1964, are clearly synonyms, appears to contain several species. These are:

(1) *Theledera abusherai* (Nagaty & Abdel Aal, 1964) n. comb., a poorly described species from *Platax* sp. in the Red Sea. It is similar to *T. pectinata*.
(2) *Theledera acanthocephala* (Stossich, 1887) n. comb., a poorly known species found in various teleosts in the Mediterranean and Red Seas.
(3) *Theledera kuhliae* (Yamaguti, 1970) n. comb., from *Kuhlia sanvicensis* off Hawaii.
(4) *Theledera plataxi* (Nagaty & Abdel Aal, 1964) n. comb., a poorly described species from *Platax* sp. in the Red Sea. It is similar to *T. pectinata*.
(5) *Theledera pectinata* (Linton, 1905) Linton, 1910; the type-species of the genus. It is known to occur in *Chloroscombrus* and *Auxis* off the eastern coast of the USA. Most of the records of this species are in fact *Tergestia manteri* (see Dollfus, 1973).
(6) *Theledera priacanthi* (MacCallum, 1917) n. comb., from *Priacanthus cruentatus* off New York, USA.
(7) *Theledera skrjabini* (Koval & Zarichkova, 1964) n. comb., from *Symphodus* [=*Crenilabrus*] *tinca* in the Black Sea. Specimens recorded from the same host in the Mediterranean by Sey (1968) as *Tergestia laticollis* may be the same species. *T. skrjabini* appears to be similar to *T. pectinata* and somewhat similar to *T. acanthocephala*.
(8) *Theledera karachiense* Bilqees, 1978, from *Stromateus sinensis* off Pakistan.

It seems likely that many of the species of this genus are synonymous.

Genus *TERGESTIA* Stossich, 1899

DIAGNOSTIC FEATURES. Cephalic lobes around oral sucker present. Six muscular flanges ('collarettes') present on each lateral surface at level of pharynx. Intestinal bifurcation in hindbody or postero-dorsal to ventral sucker. Cirrus-sac normally distinctly bipartite. Tendency for uterus to extend into post-testicular field in mature worms.

TYPE-SPECIES. *Tergestia laticollis* (Rudolphi, 1819) (type by subsequent designation: Yamaguti, 1953*a* : 26).

COMMENT. The species we include in this genus are:
(1) *Tergestia acuta* Manter, 1947; from *Caranx* spp. off Florida, Jamaica and Belize.
(2) *Tergestia agnostomi* Manter, 1954; recorded as an immature form from both the teleost *Aldrichetta forsteri* (see Angel, 1960) and the ctenophore *Pleurobrachia pileus* (see Boyle, 1966) off New Zealand. The gravid worm has been described by Jones (1978) from *A. forsteri*.
(3) *Tergestia clonacantha* Manter, 1963; from *Hemirhamphus* spp. off Fiji, New Caledonia and India.
(4) *Tergestia haswelli* Dollfus, 1927; known only as a cercaria from *Mytilus latus*, New Zealand. We are tentatively retaining this species in *Tergestia*.
(5) *Tergestia manteri* Dollfus, 1973; from various teleosts off the eastern coast of the USA and Puerto Rico. This is a new name for *Tergestia pectinata* of Manter (1947), Hopkins (1940) and Siddiqi & Cable (1960).
(6) *Tergestia magna* Korotaeva, 1972; from *Plagiogeneion macrolepis* and *Emmelichthys nitidus* in the Great Australian Bight.
(7) *Tergestia mauritanica* Dollfus, 1973; from *Pomatomus saltator* (=*saltatrix*) off Mauritania.
(8) *Tergestia pauca* Teixeira de Freitas & Kohn, 1965; from *Scombroides* sp. off Brazil.
(9) *Tergestia laticollis* (Rudolphi, 1819) Stossich, 1899; type-species of the genus (see below). *Tergestia acanthogobii* Yamaguti, 1938, from *Acanthogobius flavimanus* off Japan is herein considered to be a synonym of this species.

As with *Theledera*, it is likely that many of the above species are synonyms.

Tergestia laticollis (Rudolphi, 1819) Stossich, 1899

Distoma laticolle Rudolphi, 1819.
Echinostoma laticolle (Rudolphi) Parona, 1899.
Distoma polonii Molin of Olsson (1868).
Tergestia acanthogobii Yamaguti, 1938.
Tergestia acanthocephala (Stossich) of Baylis (1939).

TYPE-HOST AND LOCALITY. *Trachurus trachurus*, Rimini, Italy.

RECORDS
(i) Material studied
(a) From NE Atlantic region

Scomber scombrus [stomach] Plymouth, Devon, England. Collected by P. G. Corbin (see Baylis, 1939 : 482; as *Tergestia acanthocephala;* and Prudhoe & Baylis, 1957 : 83). BM(NH) 1937.8.6.141.

Trachurus trachurus [intestine] Firth of Forth, Scotland (Aug., 1963). Collected by K. MacKenzie. BM(NH) 1977.6.17.1.

—— [intestine] Bay of Biscay (46°N, 03°W; depth 132–136 m; Jan., 1971). BM(NH) 1977.6.17.2.

—— [intestine] Plymouth, Devon, England (May, 1972). BM(NH) 1977.6.17.3–10.

—— [rectum & intestine] Off NW Scotland (58°N, 08°W; depth 116–120 m; July, 1976; and 59°N, 05°W; depth 92–120 m; July, 1976). BM(NH) 1977.6.17.11–14.

—— [intestine] Vinga, west coast of Norway (Oct., 1973). Material of J. Thulin.

(b) From elsewhere
Nil

(ii) NE Atlantic records from the literature

Scomber scombrus [stomach] Plymouth, Devon, England. Baylis (1939 : 482; as *Tergestia acanthocephala*; material redetermined by Prudhoe & Baylis, 1957 : 83).

Trachurus trachurus [intestine] Bergen, Norway. Olsson (1968 : 29; as *Distoma polonii*; material redetermined by Odhner, 1911*a*, : 112).
—— [?] Wimereux, Pas de Calais, France. Monticelli (1890 : 422; as *Distomum laticolle*).
—— [intestine] Aberdeen, Scotland. Nicoll (1913 : 192).
—— [intestine] Plymouth, Devon, England. Nicoll (1914 : 483).
—— [intestine] Strait of Gibraltar. Kovaleva (1969 : 132; 1970*a* : 53).

ASPECTS OF BIOLOGY. There is one record which is probably of a cercaria of the genus *Tergestia* in the northeast Atlantic region. This is of a free-floating form off the coast of Portugal which was referred to by Kent (1871 : 270) as a larva of '*Echinorhynchus*'. It was named *Cercaria kenti* by Dollfus (1927 : 112). The complete life-history of members of this genus is, however, not known, although sporocysts have been recorded in the mussel *Mytilus* (Haswell, 1902; Angel, 1960) in New Zealand and, in addition to the record above, cercariae have been found free in plankton by Dubois *et al.* (1952), as *Cercaria mathiasi*, in the Mediterranean Sea. The cercaria bears the characteristic ring of muscular lobes around the oral sucker and the row of collarettes in the 'neck'-region; but, according to Angel (1960), 'the unique feature of the cercaria is the tail, in which, between the main stem and the body of the cercaria, is an inflated region bearing a prominent crest dorsally'. Angel also notes that 'Haswell's observations regarding the presence of "cystogenic" cells throughout the body of *Cercaria haswelli* suggests that there is a true cyst stage'. The only record of a metacercaria, however, is of *T. agnostomi* unencysted in the gastrovascular system of the ctenophore *Pleurobrachia pileus* (see Boyle, 1966) also from off New Zealand.

Tergestia laticollis is found mainly in carangid fishes and, in our area, almost entirely in *Trachurus trachurus*. It is widely distributed in the northern hemisphere, having been recorded in the Atlantic as far south as Morocco, the Caribbean, Mediterranean and Black Seas, in the Pacific Ocean as far south as the South China Sea and Hawaii and in the Indian Ocean; but it has not been found in arctic waters. The latter phenomenon is probably because its fish-hosts tend to be restricted to temperate and tropical waters.

PREVIOUS DESCRIPTIONS. Olsson (1868 : 29; as *Distoma polonii*); Monticelli (1890 : 422; as *Distomum laticolle*); Odhner (1911*a* : 111); Nicoll (1913 : 192); Vlasenko (1931 : 101); Yamaguti (1934 : 409; 1938 : 96, 97, as *Tergestia acanthogobii*; 1940 : 88; 1951 : 271; 1970 : 39); Manter (1940 : 408; 1947 : 322); Skrjabin & Koval (1957 : 426); Siddiqi & Cable (1960 : 284, figure only); Mazza (1963 : 441); Nikolaeva (1963 : 414); Sey (1968 : 8); Dollfus (1973 : 284).

DESCRIPTION (Figs 18 & 19). The material studied comprised 19 specimens of which 3 were serially sectioned. The worms are elongate and cylindrical in cross-section. Their dimensions are included in Table 14. The widest point of the body may occur at the level of the ventral sucker (Fig. 18a), or further back in the hindbody. The body surface is smooth; but the oral sucker is surrounded by a ventrally interrupted 'halo' of 13 muscular projections (lobes). Each lobe is a roughly conical, muscular body which is overlain with tegument (Fig. 18d). The musculature is similar to that of the oral sucker; but, although the bases of the 13 lobes are fused and lie close to this sucker, they are not continuous with it. A small tegumental papilla is sometimes visible ventral to the ring of lobes. In addition, 6 flanges or 'collarettes' of histologically similar construction lie along the body-surface on either side of the pharynx and/or the oral sucker (Fig. 18e). The body-wall of this worm contains prominent diagonal muscles. The *oral sucker* is slightly longitudinally elongate with a slit-like almost terminal or subterminal opening. The *ventral sucker* is more or less globular and possesses a narrow opening, which may face forwards, backwards or laterally. It is wider than the oral sucker in the ratio of about 1 : 1·1–1·6 (1·1–1·6 in contracted specimens; 1·3–1·6 in well-fixed specimens; 1·75 in a flattened specimen), and occurs well inside the anterior half of the body. There is no prepharynx, the oral sucker leading directly into a large, elongate *pharynx*. This in turn leads into a long, narrow oesophagus, which reaches back into the anterior hindbody or postero-dorsally to the ventral sucker before bifurcating. The two narrow caeca extend back almost to the posterior extremity of the body before terminating blindly.

The terminal *excretory pore* leads into a 'Y'-shaped vesicle, which was traced as far forward as

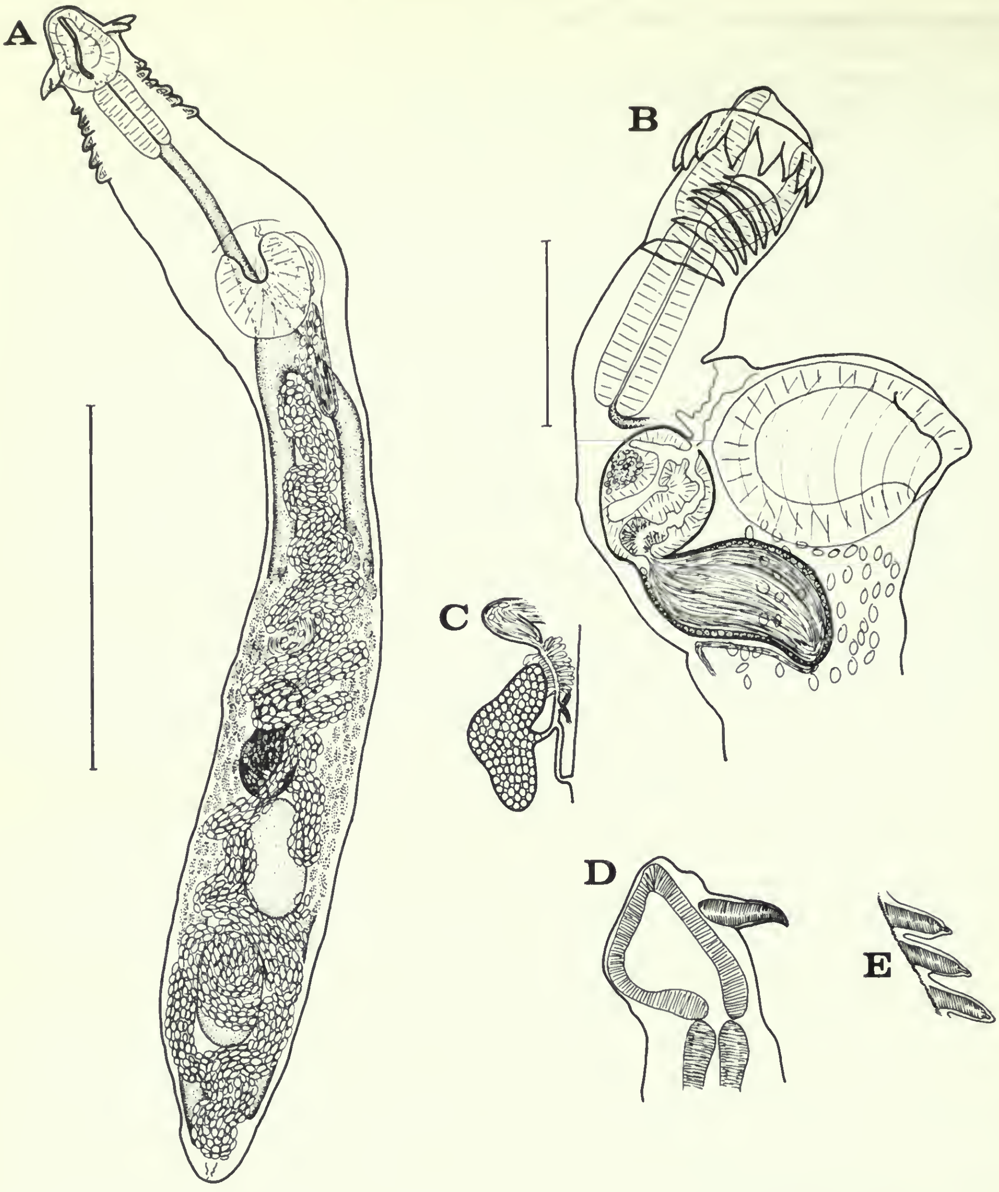


Fig. 18 *Tergestia laticollis:* (a) specimen from *Trachurus trachurus*; (b) forebody showing cirrus-sac; (c) diagram of female proximal genitalia; (d) section of anterior part of worm showing papilla-like protuberance; (e) section of 'collarettes'. Bar scale: a = 1 mm; b = 0·2 mm.

the posterior testis in a sectioned mature specimen before being obliterated by eggs. Two narrow, muscular arms were traced from the anterior hindbody as far forwards in the forebody as the level of the pharynx. Indications from the literature are that the bifurcation occurs somewhere near the middle of the hindbody.

The two *testes* are irregularly oval to elongate oval and lie almost in tandem to obliquely in the posterior half of the hindbody. The union of the vasa efferentia was not traced, but a single muscular tube has been traced from the proximal end of the withdrawn cirrus-sac, along the dorsal surface, and then passing posteriorly. The *cirrus-sac* is clearly divided into two distinct parts (Fig. 18b). The proximal part is elongate and normally reaches well into the hindbody. It contains an elongate, saccular seminal vesicle, which is surrounded by a layer of what are probably prostatic gland-cells. The distal part of the cirrus-sac is globular, and contains the pars prostatica and ejaculatory duct. The pars prostatica is small, vesicular and possesses an indistinct lining. There are also gland-cells in the distal region of the cirrus-sac (Fig. 18b), and these may also be prostatic. The ejaculatory duct is well developed, large, wide and deeply diverticulate (Fig. 18b). During copulation it appears that the whole of the ejaculatory duct is extruded through the genital pore to form a large, complex and deeply lobed cirrus. This condition is also visible in some fixed specimens (Fig. 19). When this extrusion occurs the proximal part of the cirrus-sac is pulled anteriorly to lie antero-dorsally to the ventral sucker. At rest, however, the ejaculatory duct opens into the base of a deep genital atrium, which itself opens via the genital pore ventrally and sinistrally submedian in the posterior forebody.

Table 14 Dimensions of *Tergestia laticollis* from the present material and from the literature

Authority	Odhner (1911*a*)	Yamaguti (1951)	Present material	Present material
Name used	*Tergestia laticollis*	*Tergestia laticollis*	*Tergestia laticollis*	*Tergestia laticollis*
Hosts	*Trachurus trachurus*	*Caranx equula*	*Scomber scombrus*	*Trachurus trachurus*
Locality	Palermo, Trieste	Japan	Plymouth	see text
Length (mm)	up to 4 mature at 1·5	1·6–3·5	0·97	0·80–4·6
Breadth (mm)	0·2–0·33	0·3–0·6	0·46	0·26–0·76
Length : forebody ratio	(1 : 0·26)	–	1 : 0·33	1 : 0·20–0·31
Oral sucker (mm)	0·16–0·18	0·16–0·28 × 0·13–0·23	0·17 dia.	0·16–0·21 × 0·14–0·24
Ventral sucker (mm)	0·17–0·20 × 0·20–0·23	0·30–0·46 × 0·27–0·50	0·27 × 0·22	0·18–0·37 × 0·20–0·41
Sucker ratio	(1 : 1·06–1·1)	(1 : 1·65–1·88)	1 : 1·6	1 : 1·1–1·75
Pharynx (mm)	0·08–0·10 × 0·17–0·25	0·17–0·23 × 0·08–0·13	0·10 × 0·15	0·18–0·26 × 0·07–0·12
Oesophagus (mm)	–	0·6–1·1	0·22	0·61–0·90
Cirrus-sac (mm)	–	0·26–0·53 × 0·04–0·08	–	0·30–0·74 × 0·17–0·28
Testes (mm)	–	0·16–0·40 × 0·075–0·25	–	0·10–0·25 × 0·095–0·39
Ovary (mm)	–	0·17–0·33 × 0·10–0·15	–	0·13–0·23 × 0·12–0·35
Eggs (µm)	21–23 × 15	24 × 15–18 (alive) 21–30 × 16–18 (fixed)	23–24 × 13–15	24–28 × 14–17

The elongate-oval or roughly reniform *ovary* lies anteriorly to the testes in about the middle of the hindbody. The oviduct arises from the concave dorsal surface and passes towards Mehlis' gland which lies dorso-laterally to the ovary. Prior to entering Mehlis' gland it receives firstly Laurer's canal and then the common vitelline duct. Laurer's canal is short and opens dorsally at about the level of the posterior margin of the ovary (Fig. 18c). The *uterus* passes forward from Mehlis' gland, initially forming a tightly convoluted uterine seminal receptacle. Before reaching the ventral sucker it loops posteriorly and passes to the posterior extremity, whereupon it loops forward again, thus filling much of the available space in the hindbody. In larger mature specimens the uterus reaches into the region posterior to the testes. At about the level of the ventral sucker it forms a narrow, muscular metraterm, which passes forward dorsally or dorso-laterally

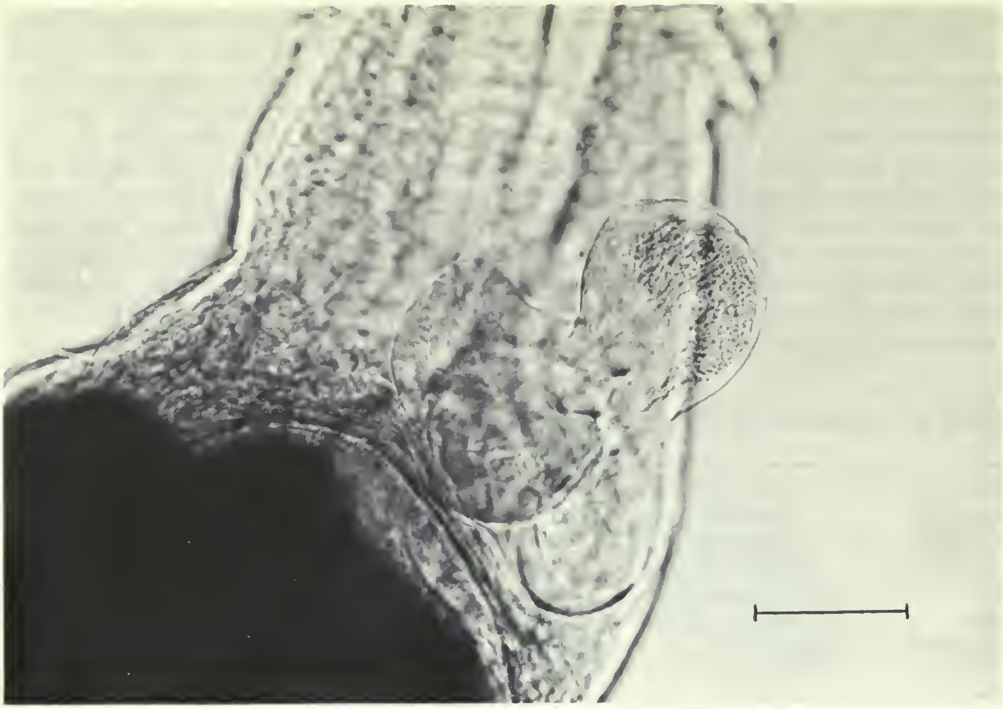


Fig. 19 Forebody of *Tergestia laticollis* with everted lobate cirrus. Bar scale: = 0·1 mm.

to this sucker and enters the base of the genital atrium. The uterus contains numerous operculate eggs. The *vitellarium* consists of a system of irregular, elongate follicles in two symmetrical, lateral fields. The extent of these fields is variable. Anteriorly the fields may only reach as far as midway between the ovary and the ventral sucker; but, in smaller and contracted specimens, the vitellarium may extend right up to the ventral sucker. The posterior limit of the fields varies between the posterior margins of either of the testes. There are also follicles in the mid-dorsal region of the body at the anterior of the vitellarium; thus in this region the fields are usually confluent. The main lateral vitelline ducts unite at about the level of the anterior margin of the ovary to form a short, simple common duct.

Discussion. *Tergestia* can conveniently be split into three groups on the basis of sucker-ratios, although the status of these groups is far from clear. In two species, *T. agnostomi* and *T. haswelli*, the ventral sucker is smaller than the oral sucker; the latter is known only as an immature form, and it is possible that allometric growth occurs. Another group of species, which include *T. manteri*, *T. mauritanica*, *T. pauca* and probably *T. laticollis* of Yamaguti (1938, 1940, 1970), have a ventral sucker which is about twice the size of the oral sucker. The remainder of the species have sucker-ratios between 1 : 1 and 1 : 1·7. Our material indicates that this is about the normal variation of *T. laticollis* in the northeast Atlantic region. *T. laticollis* differs from the other species in this group thus:

(1) *T. acuta* Manter, 1947; this species has a sucker-ratio of 1 : 1·7, which is at the upper limit of the variation in our material of *T. laticollis*; the hindbody is small and pointed; and the eggs (17–19 × 9–10 μm) are smaller.

(2) *T. clonacantha* Manter, 1963; the proportion of the uterus posterior to the testes is greater in this species; the eggs (15–17 × 9–12 μm) are smaller; and in some specimens the vitelline follicles reach close to the posterior extremity. Hafeezullah & Siddiqi (1970) figure this species from India, but Dollfus (1973) considered that these are not *T. clonacantha*, as 'les lobes céphalique sont très différents et les protubérances collaires ont un emplacement un peu différent'. It appears, however, that Manter's description of the cephalic lobes as being

11 in number, with the two inner (ventral) lobes divided, is nothing more than a description of the normal condition of this genus, where, in fact, all of the 13 lobes are joined at their bases. In addition, the position of the collarettes in this genus is variable, as can be seen in our figures of *T. laticollis*: in two specimens fixed in the same way, one has the 'collarettes' reaching back to the level of the base of the pharynx (Fig. 18a) and the other has most of the 'collarettes' lateral to the oral sucker (Fig. 18b).

(3) *T. magna* Korotaeva, 1972; this species is similar to *T. laticollis*; but the eggs are smaller (quoted as 11–18 × 11–15 µm; 12 × 12 µm in life); and the edges of the 'collarettes' are crenulate.

Yamaguti (1938) provisionally considered his *T. acanthogobii* as distinct from *T. laticollis* 'because of its entirely different habitat'. Morphologically it is indistinguishable from *T. laticollis*, and we, therefore, consider it to be a synonym. The position of the three lots of *T. laticollis* described by Yamaguti (1938, 1940, 1951) with apparent sucker-ratios of almost 1 : 2, is problematical; but, as these worms are not illustrated and as we have calculated these ratios from the range of sucker-sizes given, we are not inclined to place too much emphasis on this difference. It may well be that the sucker-ratio is an unreliable feature as far as this genus is concerned, especially if the worms are flattened, and that many of the species are conspecific with *T. laticollis*.

With reference to the previous descriptions, Mazza (1963) gave the egg-measurements of *T. laticollis* as being 82–86 × 32–34 µm and Sey (1968) gave the oral sucker-size as being 5·5 mm; both of these must be considered as either typographical or technical errors. Sey (1968) also gave a measurement of 0·046–0·080 mm for the oesophagus, which suggests that it is short and, therefore, bifurcates in the forebody. This being the case, Sey could well have been dealing with specimens of *Theledera skrjabini* (see p. 275), which is found in similar hosts in the Black Sea.

Host–parasite list

Order Clupeiformes

Alepocephalus bairdii Goode & Bean : *Olssonium turneri* gen. et sp. nov.
Steringophorus pritchardae (Campbell).
Alosa alosa (Linnaeus) : *Pronoprymna ventricosa* (Rudolphi).
Alosa fallax (Lacepéde) : *Pronoprymna ventricosa* (Rudolphi).
Sprattus sprattus (Linnaeus) : *Pronoprymna ventricosa* (Rudolphi).
Xenodermichthys socialis Vaillant : *Steringophorus blackeri* Bray.

Order Notacanthiformes

Polyacanthonotus rissoanus (Filippi & Verany) : *Prudhoeus nicholsi* gen. et sp. nov.

Order Gadiformes

Ciliata mustela (Linnaeus) : *Steringotrema divergens* (Rudolphi).
(?) *Gadus morhua* Linnaeus : *Steringophorus furciger* (Olsson).
Onogadus argentatus (Reinhardt) : *Steringophorus thulini* sp. nov.
Rhinonemus cimbrius (Linnaeus) : *Steringophorus thulini* sp. nov.
Trachyrincus trachyrincus (Risso) : *Steringophorus thulini* sp. nov.

Order Zeiformes

Capros aper (Linnaeus) : *Steringotrema divergens* (Rudolphi).

Order Perciformes

Anarhichas denticulatus Krøyer : *Steringophorus furciger* (Olsson).
Anarhichas lupus Linnaeus : *Fellodistomum fellis* (Olsson).
Steringophorus agnotus (Nicoll).
Anarhichas minor Olafsen : *Fellodistomum fellis* (Olsson).
Steringophorus agnotus (Nicoll).

Blennius ocellaris Linnaeus : *Steringotrema divergens* (Rudolphi).
Crystallogobius linearis (von Düben) : *Monascus filiformis* (Rudolphi).
Lycenchelys sarsi Collett : *Steringophorus furciger* (Olsson).
Lycodes esmarki Collett : *Steringophorus furciger* (Olsson).
Lycodes pallidus Collet : *Steringophorus furciger* (Olsson).
Lycodes vahli Reinhardt : *Steringophorus furciger* (Olsson).
Steringotrema ovacutum (Lebour).
Lycodes sp. : *Steringophorus furciger* (Olsson).
Pagellus bogaraveo (Brünnich) : *Steringotrema pagelli* (van Beneden).
Pomatoschistus minutus (Pallas) : *Monascus filiformis* (Rudolphi).
Scomber scombrus Linnaeus : *Tergestia laticollis* (Rudolphi).
Spondyliosoma cantharus (Linnaeus) : *Steringotrema pagelli* (van Beneden).
Trachurus trachurus (Linnaeus) : *Monascus filiformis* (Rudolphi).
Tergestia laticollis (Rudolphi).

Order Atheriniformes

Atherina presbyter Cuvier : *Bacciger bacciger* (Rudolphi).

Order Scorpaeniformes

Gymnacanthus tricuspis (Reinhardt) : *Steringophorus furciger* (Olsson).

Order Pleuronectiformes

Arnoglossus laterna (Walbaum) : *Monascus filiformis* (Rudolphi).
Buglossidium luteum (Risso) : *Monascus filiformis* (Rudolphi).
Glyptocephalus cynoglossus (Linnaeus) : *Monascus filiformis* (Rudolphi).
Steringophorus furciger (Olsson).
Hippoglossoides platessoides (Fabricius) : *Steringophorus furciger* (Olsson).
Steringotrema ovacutum (Lebour)
Limanda limanda (Linnaeus) : *Monascus filiformis* (Rudolphi).
Steringophorus furciger (Olsson).
Steringotrema ovacutum (Lebour).
Steringotrema pagelli (van Beneden).
Microstomus kitt (Walbaum) : *Steringophorus furciger* (Olsson).
Steringotrema pagelli (van Beneden).
Pleuronectes platessa Linnaeus : *Steringophorus furciger* (Olsson).
Steringotrema pagelli (van Beneden).
Reinhardtius hippoglossoides (Walbaum) : *Steringophorus furciger* (Olsson).

Order Lophiiformes

Lophius piscatorius Linnaeus : *Steringophorus furciger* (Olsson).

Acknowledgements

The authors are especially grateful to Mr J. Thulin, University of Gothenburg, Sweden, for generously lending us his valuable collection of fellodistomids, without which this contribution would have been much less complete. We would also like to thank the following: Dr A. V. Gaevskaja, AtlantNIRO, Kaliningrad, USSR, for presenting to us and examining for us specimens of *Pronoprymna;* Dr L. Margolis, Pacific Biological Station, Nanaimo, Canada, for lending specimens of *Pronoprymna* and *Bacciger*; Dr C. R. Kennedy, University of Exeter, for donating specimens of *Pronoprymna*; Professor J. Llewellyn, University of Birmingham, and Dr F. R. Stranack, Portsmouth College of Technology, for lending specimens of *Proctoeces;* Dr R. A. Campbell, Southeastern Massachusetts University, North Dartmouth, USA, for lending specimens of *Abyssotrema*; Dr F. Gudmundsson, Museum of Natural History, Reykjavik, Iceland, for lending the specimen of *Yamagutia*; and both Dr R. A. Matthews, Plymouth Polytechnic, for examining *Atherina* for *Bacciger* and Mrs E. A. Harris, British Museum (Natural History), for attempting to find specimens of *Scrobicularia* infested with *Proctoeces* on our behalf.

We are also indebted to the following: Mr A. C. Wheeler, British Museum (Natural History), for permission to dissect fishes in the Museum's collection; Mr D. W. Cooper and Mr S. J. Moore, British Museum (Natural History), for the preparation of serial sections; the staff of the MAFF Fisheries Laboratory, Lowestoft, and the crew of the RV *Cirolana* for their help to one of us (R. A. B.) on various cruises; the Staff of the Marine Biological Association Laboratory, Plymouth, for help to one of us (D. I. G.) during visits in 1972; and the Staff of the Parasitology Section, DAFS Marine Laboratory, Aberdeen, for their kind help to both of us during visits in 1973 and 1977.

References

Aldrich, L. E., Jr. 1961. Two new digenetic trematodes from marine fishes of Puget Sound, Washington. *J. Parasit.* **47** : 77–80.

Angel, L. M. 1960. *Cercaria haswelli* Dollfus, 1927; a re-examination of Haswell's material, with discussion of the genus *Tergestia. In Libro homenaje al Dr. Eduardo Caballero y Caballero, Jubileo 1930–1960* : 75–86. Mexico.

—— 1971. *Burnellus* gen. nov. (Digenea : Fellodistomatidae), the life history of the type-species, *B. trichofurcatus* (Johnston & Angel, 1940), and a note on a related species, *Tandanicola bancrofti* Johnston, 1927, both from the Australian freshwater catfish, *Tandanus tandanus. Parasitology, Cambridge* **62**: 375–384.

Anker, J. 1950. *Otto Friderich Müller's 'Zoologia Danica'*. Library Research Monograph Vol. 1 xiv+ 108 pp. Copenhagen.

Armstrong, H. W. 1974. *A study of the helminth parasites of the family Macrouridae from the Gulf of Mexico and Caribbean Sea: Their systematics, ecology and zoogeographical implications.* Ph.D. Thesis. Texas A & M University 329 pp.

Atkins, D. 1931. On abnormal conditions of the gills in *Mytilus edulis*. II. Structural abnormalities with a note on the method of division of the mantle cavity in normal individuals. *J. mar. biol. Ass. U.K.* **17** : 489–543.

Bae, P. A., Kang, P. A. & Kim, Y. 1977. Studies on the *Cercaria pectinata* infection to hard clam, *Meretrix lusoria. Bull. Fish. Res. Dev. Ag.* **18** : 131–140.

Baer, J. & Joyeux, C. 1961. Classe des trématodes (Trematoda Rudolphi). *In* P.-P. Grassé (Ed.), *Traité de zoologie* **4** : 561–692. Paris.

Barrington, E. J. W. 1957. The alimentary canal and digestion. *In* M. E. Brown (Ed.), *The physiology of fishes* **1** : 109–161. New York.

Baylis, H. A. 1915. A trematode from *Protopterus. Ann. Mag. nat. Hist.* (ser. 8) **16** : 85–96.

—— 1939. Further records of parasitic worms from British vertebrates. *Ann. Mag. nat. Hist.* (ser 11) **4** : 473–498.

—— **& Jones, E. I.** 1933. Records of parasitic worms from marine fishes at Plymouth. *J. mar. biol. Ass. U.K.* **18** : 627–634.

Bazikalova, A. Y. 1932. [Studies on the parasitology of Murmansk fishes.] *Sb. nauchno-promȳsl. Rabot Murmane* : 136–153. (In Russian.)

Beneden, P. J. van. 1871. Les poisson des côtes de Belgiques, leurs parasites et leurs commenseaux. *Mém. Acad. r. Sci. Lett. Belg.* **38** : 1–100.

Bilqees, F. M. 1976. A new trematode genus *Pseudohypertrema* (Fellodistomidae Nicoll, 1909) from fishes of the Karachi coast. *Norw. J. Zool.* **24** : 201–203.

—— 1978. *Tergestia karachiense* sp. n. (Trematoda, Fellodistomidae) from the fish *Stromateus sinensis* off the Karachi coast. *Zoologica Scr.* **7** : 255–256.

Blainville, H.-M. de 1820. Fasciole, *Fasciola. Dictionnaire de Sciences naturelles* **16** : 198–204. Paris & Strasbourg.

Boyle, M. S. 1966. Trematode and nematode parasites of *Pleurobrachia pileus* O. F. Muller in New Zealand waters. *Trans. R. Soc. N.Z.* (Zool.) **8** : 51–62.

Bray, R. A. 1973. Some digenetic trematodes in fishes from the Bay of Biscay and nearby waters. *Bull. Br. Mus. nat Hist.* (Zool.) **26** : 149–183.

—— 1979. Digenea in marine fishes from the eastern seaboard of Canada. *J. nat. Hist.* **13** : 399–431.

—— **& Gibson, D. I.** 1977. The Accacoeliidae (Digenea) of fishes from the north-east Atlantic. *Bull. Br. Mus. nat. Hist.* (Zool.) **31** : 51–99.

Brinkmann, A., Jr. 1956. Trematoda. *Zoology Iceland* **2** (2) : 1–34.

—— 1975. Trematodes from Greenland. *Meddr Grønland* **205** (2) : 1–88.

Caballero y C., E. 1959. Consideraciones en torno a la familia Xenoperidae Poche, 1925 (Trematoda, Digenea Carus, 1863). *Revta Biol. trop.* **7** : 57–61.

—— **Bravo Hollis, M. & Grocott, R. G.** 1952. Helmintos de la Republica de Panama. III. Tres trematodos de peces marinos con descripcion de una nueva especie. *An. Inst. Biol. Univ. Méx.* **23** : 167–180.

Cable, R. M. 1953. The life cycle of *Parvatrema borinqueñae* gen. et sp. nov. (Trematoda: Digenea) and the systematic position of the subfamily Gymnophallinae. *J. Parasit.* **39** : 408–421.

—— 1954. A new marine cercaria from the Woods Hole region and its bearing on the interpretation of larval types in the Fellodistomatidae. *Biol. Bull. mar. biol. Lab. Woods Hole* **106** : 15–20.

—— 1974. Phylogeny and taxonomy of trematodes with reference to marine species. *In* W. B. Vernberg (Ed.), *Symbiosis in the sea* : 173–193. Columbia.

Campbell, R. A. 1975. *Abyssotrema pritchardae* gen. et sp. n. (Digenea: Fellodistomidae) from the deep-sea fish, *Alepocephalus agassizi* Goode and Bean, 1883. *J. Parasit.* **61** : 661–664.

Canzonier, W. J. 1972. *Cercaria tenuans*, larval trematode parasite of *Mytilus* and its significance in mussel culture. *Aquaculture* **1** : 267–278.

Ching, H. L. 1960. Some digenetic trematodes of fishes of Friday Harbour, Washington. *J. Parasit.* **46** : 241–250.

Chubrik, G. K. 1952 [The larval stage of the trematode *Fellodistomum fellis* Nicoll, 1909 from the invertebrates of the Barents Sea.] *Zool. Zh.* **31** : 653–658. (In Russian.)

—— 1966. [Fauna and ecology of trematode larvae from molluscs in the Barents and White Seas.] *Trudy̌ murmansk. biol. Inst.* **10** (14) : 78–166. (In Russian.)

Chulkova, V. N. 1939. Parasites of marine fishes in the vicinity of Batumi (Black Sea). *Uchen. Zap. leningr. gos. Univ.* (43) (ser. biol. nauk) (11) : 21–32. (In Russian.)

Chun, S.-K. & Lee, J.-B. 1976. Studies on the trematode lervae [*sic*] infected in the hard clam, *Meretrix lusoria*. *Bull. Korean Fish. Soc.* **9** : 35–42.

Cole, H. A. 1935. On some larval trematode parasites of the mussel (*Mytilus edulis*) and the cockle (*Cardium edule*). *Parasitology, Cambridge* **27** : 276–280.

Crothers, J. H. 1966. Dale Fort marine fauna. *Fld Stud.* **2** (suppl.), xxiv + 169 pp.

Dawes, B. 1947. *The Trematoda of British fishes*. 364 pp. London.

Dayal, J. & Gupta, S. P. 1954. A new trematode, *Gauhatinae* [sic] *batrachii* n. g., from the intestine of a freshwater fish, *Clarias batrachus* (Linn.), of the sub-family Haplocladinae Odhner, 1911. *Proc. Indian Sci. Congr.* (Lucknow) **40** (3) : 190.

Dennis, E. A., Sharp, M. & Douglass, R. 1974. Carbohydrate reserves and phosphatase activity in the mollusc-trematode relationship of *Mytilus edulis* L. and *Proctoeces maculatus* (Looss, 1901) Odhner, 1911. *J. Helminth.* **48** : 1–14.

Dias, A. A. & Serrano, M. D. 1972. Alteracões das branquias e parasitismo nas mexilhões (*Mytilus edulis*) da Ria de Aveiro. *Bolm. inf. Inst. Biol. marit.* (3), 82 pp.

Dolgikh, A. V. 1963. [Helminthological study of molluscs of the Crimean coast of the Black Sea.] *Problemy Parazit. Trudy̌ nauch Konf. Parazit. USSR* **4** : 188–189. (In Russian.)

—— 1965*a*. [*Larval trematodes – parasites of molluscs from the Crimean shore of the Black Sea.*] 20 pp. Sevastopol & Lvov. (In Russian.)

—— 1965*b*. [Progenetic metacercaria of the genus *Proctoeces* of Black Sea molluscs.] *Mater. Nauchn. Konf. Vses. Obshch. Gel'mint.* (2) : 84–88. (In Russian.)

—— 1966*a*. [Helminth fauna of molluscs of the family Veneridae from the oceans of the world.] *In* [*Questions of marine biology. Essays for the symposium of young scientists* (*Sevastopol*)] : 31–33. Kiev. (In Russian.)

—— 1966*b*. [Helminth fauna of molluscs from Novorossiysk Bay.] *Biol. Morya, Kiev* [Helminth fauna of animals of southern seas] : 114–133. (In Russian.)

—— 1967. On progenesis in trematodes of the genus *Proctoeces* Odhner, 1911. *Parazitologiya* **1** : 219–221. (In Russian.)

—— 1968*a*. Helminthofauna of mollusks of the northern part of the Black Sea. *Biol. Morya, Kiev* **14** : 114–126. (In Russian.)

—— 1968*b*. Some peculiarities of biology of cercariae *Bacciger bacciger* (Rud., 1819). *Biol. Morya, Kiev* **14** : 127–132. (In Russian.)

—— 1970. [Material on helminth fauna of molluscs on the Caucasian coasts of the Black Sea.] *Biol. Morya, Kiev* **20** : 3–28. (In Russian.)

Dollfus, R. P. 1925. Liste critique des cercaire marines à queue sétigère signalées jusqu'à présent. *Trav. Stn zool. Wimereux* **9** : 43–65.

—— 1927. Notules sur des cercaires Atlantiques (I–II). *Bull. Soc. zool. Fr.* **52** : 111–118.

—— 1937. Parasitologia Mauritanica helmintha. (III) Trématodes de sélaciens et de chéloniens. *Bull. Com. Etud. hist. scient. Afr. occid. fr.* **19** : 397–519.

—— 1947. Sur *Monascus filiformis* (Rudolphi, 1819) A. Looss, 1907, trématode de l'intestine de *Cepola rubescens* (L.) en Mediterranée. *Annls Parasit. hum. comp.* **22** : 319–323.

—— 1950. Trematodes récoltés au Congo belge par le Professeur Paul Brien (Mai–août 1937). *Annls Mus. r. Congo Belge*, (zool.) ser. 5 **1** (1) : 136 pp.

—— 1951. Miscellanea helminthologia maroccana. I. Quelques trématodes, cestodes et acanthocéphales. *Archs Inst. Pasteur Maroc* **4** : 104–229.

—— 1952. Miscellanea helminthologia maroccana. IV. Affinités naturelles de *Pseudochetosoma salmonicola* R. P. Dollfus (Famille Steganodermatidae nov.) – Emendation de la superfamille Haploporoidea W. Nicoll, 1935. *Archs Inst. Pasteur Maroc.* **4** : 369–386.

—— 1965. Metacercaria: *Proctoeces progeneticus* (Trematoda : Digenea) chez une *Gibbula* (Gastropoda Prosobranchiata) de la côte Atlantique du Maroc. Observations sur la famille Fellodistomatidae. *Annls Parasit. hum. comp.* (1964). **39** : 755–774.

—— 1966. Metacercaire progénétique de *Proctoeces* chez un gastropode prosobranche de la cote Atlantique du Maroc. *Proc. 1st Int. Congr. Parasit.* (Rome) **1** : 536–537.

—— 1968. Les trematodes de l'histoire naturelle des helminthes de Felix Dujardin (1845). *Mem. Mus. natn. Hist. nat. Paris* (Zool.) **54** : 119–196.

—— 1973. Du genre *Tergestia* M. Stossich 1899 (Trematoda Digenea). *Annls Parasit. hum. comp.* **48** : 275–287.

Dubois, G., Baer, J. G. & Euzet, L. 1952. Une nouvelle cercaire du plankton marin de Sète, *Cercaria mathiasi* n. sp. *Revue suisse Zool.* **59** : 503–510.

Dupouy, J. & Martinez, J. C. 1973. Action de *Proctoeces maculatus* (Looss, 1901) (Trematoda, Fellodistomatidae) sur le développement de gonads chez *Mytilus galloprovincialis* Lmk. *C. r. hebd. Sèanc. Acad. Sci., Paris* **277D** : 1889–1892.

Dyk, V. & Dyková, S. 1964. Přispěvek k znalosti helmintů pstruha a lipana řeky Savinje (SFRJ). *Sb. vys. Sk. zeměd. Brné* (rada B) **12** : 399–408.

Eremina, B. A. 1970. [The infection of certain commercial fish on the south-western coast of Africa.] *In* A. M. Parukhin (Ed.) [*Problems of marine parasitology: data of the 1st All-Union Symposium on parasites and diseases of marine animals, Sebastopol*] : 26–29. Kiev. (In Russian.)

Fischthal, J. H. & Kuntz, R. E. 1963. Trematode parasites of fishes from Egypt. Part 4. A redescription of *Monascus typicus* (Odhner, 1911) (Fellodistomidae). *Proc. helminth. Soc. Wash.* **30** : 177–182.

—— **& Thomas, J. D.** 1968. Digenetic trematodes of some freshwater and marine fish from Ghana. *Proc. helminth. Soc. Wash.* **35** : 126–140.

—— —— 1972*a*. Additional hemiurid and other trematodes of fishes from Ghana. *Bull. Inst. fond. Afr. noire* (ser. A) **34** : 9–25.

—— —— 1972*b*. Digenetic trematodes of marine fishes from Senegal. *Bull. Inst. fond. Afr. noire* (ser. A) **34** : 292–322.

Freeman, R. F. H. 1962. Volumetric respirometer measurements of the oxygen consumption of the digenetic trematode *Proctoeces subtenuis. Comp. Biochem. Physiol.* **7** : 199–209.

—— 1963*a*. Experimental infection of two species of wrasse with the digenean *Proctoeces subtenuis. J. mar. biol. Ass. U.K.* **43** : 113–123.

—— 1963*b*. Haemoglobin in the digenetic trematode *Proctoeces subtenuis* (Linton). *Comp. Biochem. Physiol.* **10** : 253–256.

—— **& Llewellyn, J.** 1958. An adult digenetic trematode from an invertebrate host: *Proctoeces subtenuis* (Linton) from the lamellibranch *Scrobicularia plana* (Da Costa). *J. mar. biol. Ass. U.K.* **37** : 435–457.

Fuhrmann, O. 1928. Zweite Klasse des Cladus Plathelminthes. *In* W. Kükenthal & T. Krumbach (Eds.), *Handbuch der Zoologie*, 140 pp. Berlin & Leipzig.

Fujita, T. 1925. Études sur les parasites de l'huitre comestible du Japon *Ostrea gigas* Thunberg. Traduction accompagnée de notes, de diagnoses et d'une bibliographie par Robert-Ph. Dollfus. *Annls Parasit. hum. comp.* **3** : 37–59.

Gaevskaja, A. V. 1972. The influence of sunlight and temperature of the water on the emergence of some species of cercariae from Black Sea molluscs. *Gidrobiol. Zh.* **8** (5) : 104–105. (In Russian; English translation: *Hydrobiol. J.* **8** (5) : 84–85.)

—— **& Kovaleva, A. A.** 1977. New species of trematodes from fishes of the Falkland–Patagonian region (south-western Atlantic). *Parazitologiya* **11** : 417–423. (In Russian.)

—— —— 1978. Materials on fish trematodes in the south-western Atlantic. *Vest. Zool.* (3) : 60–66. (In Russian.)

Giard, A. 1897. Sur un cercaire sétigère (*Cercaria lutea*), parasite des pélécypodes. *C. r. Séanc. Soc. Biol.* **49** : 954–956.

Gibson, D. I. & Bray, R. A. 1977. The Azygiidae, Hirudinellidae, Ptychogonimidae, Sclerodistomidae and Syncoeliidae (Digenea) of fishes from the northeast Atlantic. *Bull. Br. Mus. nat. Hist.* (Zool.) **32** : 167–245.

—— —— 1979. The Hemiuroidea: terminology, systematics and evolution. *Bull. Br. Mus. nat. Hist.* (Zool.) **36** (2) : 35–146.

—— —— in preparation. The Hemiuridae (Digenea) of fishes from the northeast Atlantic.

Gupta, N. K. 1956. Studies on the digenetic trematodes of marine fishes from the Gulf of Manaar (India). *Res. Bull. Panjab. Univ.* **89** : 61–83.

—— **& Miglani, A.** 1974. Digenetic trematodes from marine fishes of port Blair (Andaman Island) India. *Proc. Indian Sci. Congr.* (Nagpur) **61** (3B) : 107–108.

—— —— 1976. Digenetic trematodes from marine food fishes and wild ducks of Port Blair (Andaman and Nicobar Islands) India. *Revta ibér. Parasit.* **36** : 219–248.

Gupta, S. P. 1955. Trematode parasites of fresh-water fishes. *Indian J. Helminth.* **5** : 1–80.

Hafeezullah, M. & Siddiqi, A. H. 1970. Digenetic trematodes of marine fishes of India. Part II. Fellodistomatidae. *J. Parasit.* **56**: 932–940.

Hanson, M. L. 1950. Some digenetic trematodes of marine fishes of Bermuda. *Proc. helminth. Soc. Wash.* **17** : 74–89.

Haswell, W. A. 1903. On two remarkable sporocysts occurring in *Mytilus latus*, on the coast of New Zealand. *Proc. Linn. Soc. N.S.W.* (1902) **27** (4) : 497–515.

Hausmann, L. 1897. Ueber Trematoden der Süsswasserfische. *Revue suisse Zool.* **5** : 1–42.

Hopkins, S. H. 1940. The excretory systems of *Tergestia* Stossich, 1899 and *Cornucopula adunca* (Linton, 1905) (Trematoda). *Trans. Am. microsc. Soc.* **59** : 281–284.

Huet, L. 1891. Une nouvelle cercaire (*C. pectinata*) chez *Donax anatinum. J. anat. Physiol., Paris* **27** : 162–165.

Hureau, J. C. & Monod, T. (Eds) 1973. *Check-list of the fishes of the north-eastern Atlantic and of the Mediterranean.* Vol. 1, 683 pp. Vol. 2, 331 pp. Paris.

Ichihara, A. 1964. On an adult trematode (*Proctoeces*) obtained from the top-shell, *Turbo cornutus. Jap. J. Parasit.* **13** : 294–295. (In Japanese.)

—— 1965. On a Trematoda (*Proctoeces* sp.) of the topshell, *Turbo* (*Battilus*) *cornutus* Solander. I. Geographical distribution in Japan and observations on the adult fluke. *Jap. J. Parasit.* **14** : 426–436.

Ishii, N. 1935. Brief note on a new species of fish trematodes, *Urorchis imba. Jap. J. Zool.* **6** : 547–549.

Issaitschikov, I. M. 1928. Contributions to parasitic worms of some groups of vertebrates from Russian Arctic. *Trudȳ morsk. nauch. Inst.* **3** (2) : 1–79. (In Russian; partial English translation: 1933. *Trudȳ gos. okeanogr. Inst.* **3** (1) : 37–44.)

Jacoby, S. 1899. Beiträge zur Kenntniss einiger Distomen. *Arch. Naturgesch.* (1900) **66** : 1–30.

James, B. L., Sannia, A. & Bowers, E. A. 1977. Parasites of birds and shellfish. *In* A. Nelson-Smith & E. M. Bridges (Eds), *Problems of a small estuary.* Proceedings of symposium on the Burry Inlet (South Wales). (Swansea, 13–18 Sept., 1976), Session 6 (1), 17 pp. Swansea.

Janiszewska, J. 1953. Some Adriatic sea fish trematodes. *Zoologica Pol.* **6** : 20–48.

Jobert, 1894. Recherches pour servir à l'histoire du parasitisme. *C. r. Séanc. Soc. Biol.* **46** : 519–520.

Johnston, S. J. 1913. On some Queensland trematodes, with anatomical observations and descriptions of new species and genera. *Q. Jl microsc. Sci.* **59** : 361–400.

Johnston, T. H. 1927. New trematodes from an Australian siluroid. *Trans. R. Soc. S. Aust.* **51** : 129–136.

Jones, J. B. 1978. A redescription of *Tergestia agnostomi* Manter, 1934, based on gravid specimens (Trematoda: Fellodistomatidae). *Jl R. Soc. N.Z.* **8** : 157–159.

Kakacheva-Avramova, D. 1966*a*. *Pseudochetosoma salmonicola* Dollfus, 1951 et *Pseudochetosoma leucisci* Ergens, 1963 sont-elles des espèces differentes ? *Annls Parasit. hum. comp.* **41** : 307–312.

—— 1966*b*. On the problem whether *Pseudochetosoma salmonicola* Dollfus, 1951 and *Pseudochetosoma leucisci* Ergens, 1963 are different species. *Izv. tsent. khelmint. Lab.* **11** : 67–70. (In Bulgarian.)

Kamegai, S. 1974. Fellodistomid trematodes of deep-sea fishes from Suruga Bay, Jap. *Proc. 3rd Int. Congr. Parasit.* (Munich) **3** : 1615–1616.

Karyakarte, P. P. & Yadav, B. B. 1976. On a new and a known species of the genus *Monascus* Looss, 1907 (Trematoda : Monascidae) from marine fishes from the west coast of India. *Marathwada Univ. J. Sci.* (Nat. Sci.) **15** (Sci. 8) : 169–175.

Kent, W. S. 1871. Notes on Appendicularia and the larval condition of an acanthocephaloid scolecid from the coast of Portugal. *Q. Jl microsc. Sci.* **11** : 267–270.

Kobayashi, H. 1920. On some digenetic trematodes in Japan. *Parasitology, Cambridge* **12** : 380–410.

Køie, M. 1969. On the endoparasites of *Buccinum undatum* L. with special reference to the trematodes. *Ophelia* **6** : 251–279.

—— 1979. On the morphology and life-history of *Monascus* [=*Haplocladus*] *filiformis* (Rudolphi, 1819) Looss, 1907 and *Steringophorus furciger* (Olsson, 1868) Odhner, 1905 (Trematoda, Fellodistomidae). *Ophelia* **18** : 113–132.

Komiya, Y. 1965. Metacercariae in Japan and adjacent territories. *Prog. Med. Parasit. Japan* **2** : 1–328.

Korotaeva, V. D. 1972. New species of Trematoda of the genus *Tergestia* Stossich, 1899 (Trematoda, Fellodistomatidae). *Izv. tikhookean. nauchno issled. Inst. rȳb. Khoz. Okeanogr.* **81** : 263–266. (In Russian.)

Korringa, P. 1952. Recent advances in oyster biology (concluded). *Q. Rev. Biol.* **27** : 339–365.

Koval, V. P., Paschkevitschute, A. S., Boschko, E. G., Kovalenko, A. A. & Stavrovsky, K. B. 1973. [The parasite fauna of Kakhovska reservoir in the sixteenth year of its existence.] *Visn. kȳyiv. Univ.* **15** (ser. biol.): 135–138. (In Ukrainian.)

—— **& Zarichkova, D. B.** 1964. [A study of the trematodes of fishes from the Black Sea.] *Visn. kȳyiv. Univ.* **6** (ser. biol.): 141–146. (In Ukrainian.)

Kovaleva, A. A. 1965. [Helminth fauna of a local school of horse mackerel in the Black Sea.] *Mater. Nauch. Konf. Vses. obschch. gel'mint.* (2) : 121–126. (In Russian.)

—— 1968. Effect of the age and food composition on helminthofauna of *Trachurus mediterraneus ponticus* Aleev. *Biol. Morya, Kiev.* **14** : 47–53. (In Russian.)

—— 1969. [Helminth fauna of *Trachurus* in the Atlantic Ocean basin.] *Mater. Nauch. Konf. Vses. obshch. gel'mint.* (1) : 129–134. (In Russian.)

—— 1970*a*. [Helminth fauna of the mackerel genus *Trachurus* (Carangidae, Perciformes) in the Atlantic Ocean basin.] *Biol. Morya, Kiev* **20** : 37–66. (In Russian.)

—— 1970*b*. [Seasonal variation in the helminth fauna of *Trachurus mediterraneus ponticus*.] *In* A. M. Parukhin (Ed.) [*Problems of marine parasitology: data of the 1st All-Union Symposium on parasites and diseases of marine animals, Sebastopol*] : 39–40. Kiev. (In Russian.)

—— 1975. [Peculiarities of the parasitofauna of the mackerel genus *Trachurus* from the Atlantic coast of Africa.] *Problemy Parazit. Trudȳ nauch. Konf. Parazit. USSR* **8** (1) : 216–217. (In Russian.)

Kumari, N. V. 1975. A new species of the genus *Monascus* Looss, 1907 (Trematoda : Digenea : Fellodistomidae) parasitic on flat fishes. *In* K. K. Tiwari & C. B. Srivastava (Eds), *Dr. B. S. Chauhan Commemoration Volume* (*presented on his 60th birthday*) : 247–250. Bhubaneswar.

Kurochkin, Y. V. 1964. [Helminth fauna of clupeid fish in the Caspian Sea.] *Trudȳ astrakh. gos. Zapov.* **9** : 164–181. (In Russian.)

Lamothe-Argumedo, R. 1969. Trematodeos de peces. IV. Registro de cuatro especies de tremátodos de peces marinos de la costa del Pacífico Mexicana. *An. Inst. Biol. Univ. Méx.* **40** : 179–194.

Lang, W. H. & Dennis, E. A. 1976. Morphology and seasonal incidence of infection of *Proctoeces maculatus* (Looss, 1901) Odhner, 1911 (Trematoda) in *Mytilus edulis* L. *Ophelia* **15** : 65–75.

Layman, E. M. 1930. Parasitic worms from the fishes of Peter the Great Bay. *Izv. tikhookean. nauchno promȳsl. Stn* **3** : 1–120 (In Russian & German.)

Lebour, M. V. 1908*a*. Fish trematodes of the Northumberland coast. *Rep. scient. Invest. Northumb. Sea Fish Comm.* (1907) : 23–67.

—— 1908*b*. Trematodes of the Northumberland coast. No. 2. *Trans. nat. Hist. Soc. Northumberland* (n.s.) **3** (1) : 28–45.

Lee, D. L. & Smith, M. H. 1965. Hemoglobins of parasitic animals. *Expl Parasit.* **16** : 392–424.

Lespes, P. G. C. 1857. Observations sur quelques cercaires parasites de mollusques marins. *Annals Sci. nat.* (Zool. ser, 4) **7** : 113–117.

Levinsen, G. M. R. 1881. Bidrag til Kundskab om Grønlands Trematodfauna. *Overs. K. danske Vidensk. Selsk. Forh.* (1) **23** : 52–84.

Linton, E. 1905. Parasites of fishes of Beaufort, North Carolina. *Bull. Bur. Fish., Wash.* **24** : 321–428.

—— 1907. Notes on parasites of Bermuda fishes. *Proc. U.S. natn. Mus.* **33** : 85–126.

—— 1910. Helminth fauna of the Dry Tortugas. II. Trematodes. *Pap. Tortugas Lab.* **4** : 11–98.

—— 1940. Trematodes from fishes mainly from the Woods Hole region, Massachusetts. *Proc. U.S. natn. Mus.* **88** : 1–172.

Little, P. A. 1929. The trematode parasites of Irish marine fishes. *Parasitology, Cambridge* **21** : 22–30.

Loos-Frank, B. 1969. Zwei adulte Trematoden aus Nordsee-Mollusken: *Proctoeces buccini* n. sp. und *P. scrobiculariae* n. sp. *Z. Parasitenk.* **32** : 324–340.

Looss, A. 1896. Recherches sur la faune parasitaire de l'Égypte. *Mém. Inst. égypt.* **3** : 1–250.

—— 1898. Quelques observations à propos de la note: Forme nouve etc. de entozoi d'Egitto de Mr. le docteur Sonsino dans ce journal, vol. XX, 1896. *Zentbl. Bakt. ParasitKde* **23** : 453–461.

—— 1899. Weitere Beiträge zur Kenntniss der Trematoden-Fauna Aegyptens, zugleich Versuch einer natürlichen Gliederung des Genus *Distomum* Retzius. *Zool. Jb.* (Syst.) **12** : 521–784.

—— 1900. Nachträgliche Bemerkungen zu den Namen der von mir vorgeschlagenen Distomidengattungen. *Zool. Anz.* **23** : 601–608.

—— 1901. Ueber einige Distomen der Labriden des Triester Hafens. *Zentbl. Bakt. ParasitKde* **29** : 398–405.

—— 1907. Zur Kenntnis der Distomenfamilie Hemiuridae. *Zool. Anz.* **31** : 585–620.

—— 1912. Über den Bau einiger anscheinend seltner Trematoden-Arten. *Zool. Jb.* (Syst.) Suppl. **15** : 323–366.

Lopez-Roman, R. & Guevara-Pozo, D. 1974. Dos especies de trematoda del genero *Steringotrema* Odhner, 1911, parasitos de teleosteos marinos del mar de Alboran. *Revta ibér. Parasit.* **34** : 1–7.

Lühe, M. F. L. 1901. Zwei neue *Distomen* aus indischen Anuren. *Zentbl. Bakt. ParasitKde* **30** : 166–177.

—— 1906. Report on the trematode parasites from marine fishes of Ceylon. *Rep. Govt. Ceylon Pearl Oyster Fish Gulf Manaar* **5** : 97–108.

MacCallum, G. A. 1917. Some new forms of parasitic worms. *Zoopathologica* **1** : 43–75.

McLaren, D. J. & Hockley, D. J. 1977. Blood flukes have a double outer membrane. *Nature, Lond.* **269** : 147–149.

Machida, M. 1975. Two species of digenetic trematodes from marine fishes of the Tsushima Islands, with reference to Parantorchiinae. *Bull. natn. Sci. Mus. Tokyo* (ser. A, zool.) **1** : 183–189.

Madhavi, R. 1975. Digenetic trematodes from marine fishes of Waltair coast, Bay of Bengal. Family Fellodistomatidae. *Riv. Parassit.* **36** : 267–278.

—— 1976. Digenetic trematodes from marine fishes of Waltair coast, Bay of Bengal. Family Cryptogonimidae. *Riv. Parassit.* **37** : 313–322.

Mamaev, Y. L., Parukhin, A. M. & Baeva, O. M. 1963. [Parasitic worms of flat-fishes from Far Eastern seas.] *In* P. G. Oshmarin (Ed.) [*Helminths of animals of Primore and the Pacific Ocean*] : 82–113. Moscow. (In Russian.)

—— —— —— **& Oshmarin, P. G.** 1959. [*Helminth fauna of Far-eastern salmonids in connection with questions of local stocks and routes of migration of these fishes*], 74 pp. Vladivostok. (In Russian.)

Manter, H. W. 1931. Some digenetic trematodes of marine fishes of Beaufort, North Carolina. *Parasitology, Cambridge* **23** : 396–411.

—— 1934. Some digenetic trematodes from deep-water fish of Tortugas, Florida. *Pap. Tortugas Lab.* **28** : 257–345.

—— 1935. *Lomasoma*, new name for *Lomaphorus*, Manter, 1934 (Trematoda). *J. Parasit.* **21** : 220–221.

—— 1940. Digenetic trematodes of fishes from the Galapagos Islands and the neighbouring Pacific. *Allan Hancock Pacif. Exped.* 2 **14** : 329–496.

—— 1947. The digenetic trematodes of marine fishes of Tortugas, Florida. *Am. Midl. Nat.* **38** : 257–416.

—— 1954. Some digenetic trematodes from fishes of New Zealand. *Trans. R. Soc. N.Z.* **82** : 475–568.

—— 1960. Some additional Digenea (Trematoda) from New Zealand fishes. *In Libro homenaje al Dr. Eduardo Caballero y Caballero, Jubileo 1930–1960*: 197–201. Mexico.

—— 1963. Studies on digenetic trematodes of fishes of Fiji. III. Families Acanthocolpidae, Fellodistomatidae and Cryptogonimidae. *J. Parasit.* **49** : 443–450.

—— **& Pritchard, M. H.** 1962. Studies on digenetic trematodes of Hawaiian fishes: families Fellodistomatidae, Opistholebetidae and Gyliauchenidae. *Trans. Am. microsc. Soc.* **81** : 113–123.

Margolis, L. & Ching, H. L. 1965. Review of the trematode genera *Bacciger* and *Pentagramma* (Fellodistomatidae) and description of *P. petrowi* (Layman, 1930) n. comb. from marine fishes from the Pacific coast of Canada. *Can. J. Zool.* **43** : 381–405.

Martinez, J. C. 1974. La progenese dans le cycle evolutif de *Proctoeces maculatus* (Looss, 1901) Odhner, 1911 (Trematoda, Fellodistomatidae). *Bull. Soc. Hist. nat. Afr. N.* **64** (3/4) : 39–46 (also 3 pp. of figures following p. 456 in volume **65** (1975)).

Mathias, P. 1934. Sur quelques trématodes de poisson marins de la region de Banyuls. *Archs Zool. exp. gén.* **75** : 567–581.

Matricon-Gondran, M. 1965. Structure fine de la paroi du sporocyste de *Cercaria pectinata* (larve de *Bacciger bacciger* (Rud.) trématode digénétique. Steringophoridae Odhner). *Bull. Soc. zool. Fr.* **90** : 341–342.

—— 1966. Différenciation du tégument chez un trématode digénétique larvaire. *Cercaria pectinata* Huet, parasite de *Donax vittatus* Da Costa. *J. Microscopie* **5** : 62*a*–63*a*.

—— 1971. Etude ultrastructurale des récepteurs sensoriels tégumentaires de quelques trématodes digénétiques larvaires. *Z. Parasitenk.* **35** : 318–333.

Mazza, J. 1963. Quelques trématodes de poisson de l'etang de Berre. *Rev. Trav. Inst. Pêch. marit.* **27** : 441–448.

Mehra, H. R. 1963. Revision of Fellodistomoidea (syn. Fellodistomatoidea La Rue, 1957): Families Fellodistomidae Woodcock, 1912, Gymnophallidae Dollfus, 1939 and Monodhelminthidae Dollfus, 1937. *Proc. natn. Acad. Sci. India* **33B** : 361–378.

Miller, M. J. 1941. A critical study of Stafford's report on 'Trematodes of Canadian fishes' based on his trematode collection. *Can. J. Res.* **19** : 28–52.

Molin, R. 1859. Prospectus helminthum, quae in parte secunda prodromi faunae helminthologicae Venetae continentur. *Sber. Akad. Wiss. Wien.* **33** : 287–302.

—— 1861. Prodromus faunae helminthologicae Venetae adjectis disquisitionibus anatomicis et criticis. *Denkschr. Akad. Wiss. Wien.* **19** : 189–338.

Monticelli, F. S. 1890. Elenco degli elminti studiata a Wimereux nella primavera de 1889. *Bull. scient. Fr. Belg.* (ser. 4) **22** : 417–444.

—— 1891. Osservazioni intorno ad alcune forme del gen. *Apoblema* Dujard. *Atti Accad. Sci. Torino* **26** : 496–524.

—— 1893. Studii sui trematodi endoparassiti: Primo contributo di osservazioni sui distomidi. *Zool. Jb.* Suppl. **3** : 1–229.

Mortensen, T. 1920. Notes on some Scandinavian echinoderms, with descriptions of two new ophiurids. *Vidensk. Meddr dansk naturh. Foren.* **72** : 45–79.

Müller, O. F. 1776. *Zoologiae Danicae prodromus, seu animalium Daniae et Norvegiae indigenarum characteres, nomina, et synonyma imprimis popularum*, xxxii + 282 pp. Havniae.

—— 1777. *Zoologiae Danicae seu animalium Daniae et Norvegiae rariorum ac minus notorum icones.* Fasciculus primus continens tabulas I–XL, 4 pp. 40 pls. Havniae.

—— 1780. *Zoologia Danica seu animalium Daniae et Norvegiae rariorum ac minus notorum icones.* Fasciculus secundus continens tabulas XLI–LXXX, 4 pp. 40 pls. Havniae.

—— 1784. *Zoologia Danica seu animalium Daniae et Norvegiae rariorum ac minus notorum descriptiones et historia.* Volumen secundum. Explicationi iconum fasculi secundi eiusdems operis inserviens, 124 pp. Lipsiae.

Nagaty, H. F. & Abdel Aal, T. M. 1961. Trematodes of fishes from the Red Sea. 10. On three new Cryptogonimidae including two new genera. *Parasitology, Cambridge* **51** : 233–236.

—— —— 1964. Trematodes of fishes from the Red Sea. Part 11. On a new fellodistomid genus including two species. *J. Vet. Sci. U.A.R.* **1** : 11–17.

Nahhas, F. M. & Cable, R. M. 1964. Digenetic and aspidogastrid trematodes from marine fishes of Curacao and Jamaica. *Tulane Stud. Zool.* **11** : 167–228.

—— **& Powell, E. C.** 1971. Digenetic trematodes of marine fishes from the Floridian northern Gulf of Mexico. *Tulane Stud. Zool. Bot.* **17** : 1–9.

Naidenova, N. N. 1967. [Study of the helminth fauna of *Gobius niger* Linne in the Black Sea.] *Problemy Parazit. Trudȳ nauch. Konf. Parazit. USSR* **5** : 486–588. (In Russian).

—— 1970. [Parasitofauna of fish of the family Gobiidae in the Azov Sea.] *Biol. Morya, Kiev* **20** : 84–113. (In Russian.)

—— 1974. [*Parasite fauna of fishes of the family Gobiidae from the Black and Azov seas.*] 182 pp. Kiev. (In Russian.)

Nasir, P. & Gomez, Y. 1977. Digenetic trematodes from Venezuelan marine fishes. *Riv. Parassit.* **38** : 53–73.

Nelson, J. S. 1976. *Fishes of the World.* 416 pp. New York etc.

Nicoll, W. 1907. A contribution towards a knowledge of the entozoa of British marine fishes. Part 1. *Ann. Mag. nat. Hist.* (ser. 7) **19** : 66–94.

—— 1909*a*. Studies on the structure and classification of the digenetic trematodes. *Q. Jl microsc. Sci.* **53** : 391–487.

—— 1909*b*. A contribution towards a knowledge of the entozoa of British marine fishes. Part 2. *Ann. Mag. nat. Hist.* (ser. 8) **4** : 1–25.

—— 1901. On the entozoa of fishes from the Firth of Clyde. *Parasitology, Cambridge* **3** : 322–359.

—— 1912. On two new trematode parasites from British food-fishes. *Parasitology, Cambridge* **5** : 197–202.

—— 1913. Trematode parasites from food-fishes of the North Sea. *Parasitology, Cambridge* **6** : 188–194.

—— 1914. The trematode parasites of fishes from the English Channel. *J. mar. biol. Ass. U.K.* **10** : 466–505.

—— 1915*a*. A list of the trematode parasites of British marine fishes. *Parasitology, Cambridge* **7** : 339–378.

—— 1915*b*. The trematode parasites of north Queensland. III. Parasites of fishes. *Parasitology, Cambridge* **8** : 22–41.

—— **& Small, W.** 1909. Notes on larval trematodes. *Ann. Mag. nat. Hist.* (ser. 8) **3** : 237–246.

Nikolaeva, V. M. 1963. Parasitic fauna of the local schools of some pelagic fishes of the Black Sea. *Trudy̆ Sevastopol. biol. Sta* **16** : 387–438. (In Russian.)

—— **& Kovaleva, A. A.** 1966. [Parasite fauna of *Trachurus* from the Mediterranean basin.] *Biol. Morya, Kiev* [Helminthofauna of animals of the southern seas] : 67–79. (In Russian.)

Noble, E. R. & Orias, J. D. 1975. Parasitism in the bathypelagic fish, *Melanostigma pammelas. Int. J. Parasit.* **5** : 89–93.

Odhner, T. 1905. Die Trematoden des arktischen Gebietes. *Fauna arct.* **4** : 289–372.

—— 1910. Nordostafrikanische Trematoden, grösstentiels vom Weissen Nil (von der schwedischen zoologischen Expedition gesammelt). *Results Swed. zool. Exped. to Egypt and the White Nile*, 1901 **23A** : 1–170.

—— 1911*a*. Zum näturlichen System der Trematoden. III. (Ein weiterer Fall von sekundarum Anus.) *Zool. Anz.* **38** : 97–117.

—— 1911*b*. Zum näturlichen System der digenen Trematoden. IV. *Zool. Anz.* **38** : 513–531.

—— 1911*c*. Zum näturlichen System der digenen Trematoden. II. *Zool. Anz.* **37** : 237–253.

—— 1928. Weitere Trematoden mit Anus. *Ark Zool.* **20B** (2) : 1–6.

Olsson, P. 1868. Entozoa, iakttagna hos Skandinaviska hafsfiskar. 1. Platyelminthes. *Acta Univ. lund.* (1867) **4** : 64 pp.

Overstreet, R. M. 1969. Digenetic trematodes of marine teleost fishes from Biscayne Bay, Florida. *Tulane Stud. Zool. Bot.* **15** : 119–176.

—— **& Martin, D. M.** 1974. Some digenetic trematodes from synaphobranchid eels. *J. Parasit.* **60** : 80–84.

Ozaki, Y. 1925. Preliminary notes on a trematode with anus. *J. Parasit.* **12** : 51–53.

—— 1927. Two new genera of fish trematodes. *Jap. J. Zool.* **1** : 157–164.

Pagenstecher, H. A. 1862. Untersuchungen über niedere Seethiere aus Cette. *Z. wiss. Zool.* **12** : 265–311.

Palombi, A. 1931*a*. Per una migliore conoscenza dei Trematodi endoparassiti dei pesci del golfo di Napoli. I. – *Steringotrema divergens* (Rud.) e *Haploporus benedeni* (Stoss.). *Annuar. Mus. zool. Univ Napoli* (NS) **6** : 1–15.

—— 1931*b*. La copulazione nei Trematodi. Ricerche sul significato fisiologico del canal di Laurer. *Archo zool. ital.* **17** : 123–151.

—— 1932. *Bacciger bacciger* (Rud.) Nicoll, 1914 forma adulta di *Cercaria pectinata* Heut, 1891. *Boll. Soc. Nat. Napoli* **44** : 217–220.

—— 1933. *Cercaria pectinata* Huet e *Bacciger bacciger* (Rud.). Rapporti genetici e biologia. *Boll. Zool.* **4** (1) : 1–11.

—— 1934*a*. *Bacciger bacciger* (Rud.) trematode digenetico: fam. Steringophoridae Odhner. Anatomia, sistematica e biologia. *Pubbl. Staz. zool. Napoli* **13** : 438–478.

—— 1934*b*. Gli stadi larvali dei Trematodi del golfo di Napoli. 1. Contributo allo studio della morfologia, biologia e sistematica della cercarie marine. *Pubbl. Staz. zool. Napoli* **14** : 51–94.

—— 1940. Gli stadi larvali dei Trematodi del golfo di Napoli. 3° Contributo allo studio della morfologia, biologia e sistematica delle cercarie marine. *Riv. Parassit.* **4** : 1–25.

Papoutsoglou, S. E. 1976. Metazoan parasites of fishes from Saronicos Gulf, Athens – Greece. *Thalassographica* **1** : 69–102.

Parona, C. 1899. Catologo di elminti raccolti in vertebrati dell'Isola d'Elba dal Dott. Giacomo Damiani. *Boll. Musei Lab. Zool. Anat. comp. R. Univ. Genova* (77) : 16 pp.

—— 1912. *L'elmintologia italiana da'suoi primi tempi all'anno* 1910. *Bibliografia, sistematica, corologia storia. Vol.* 2. *Sistematica, corologia, storia*, 540 pp. Novara. [n.v.].

Parukhin, A. M. 1970. [On the study of the trematode fauna in fish from the Red Sea and Aden Bay.] *Biol. Morya, Kiev* **20** : 187–213. (In Russian.)

—— 1971. [A study on the trematode fauna of fishes of the Red Sea and Aden Bay.] *Biol. Morya, Kiev* **25** : 136–146. (In Russian.)

—— 1973. [On the age dynamics of the parasite infection of *Trachurus trachurus* and *Nemipterus japonicus* from two regions of the Indian Ocean.] *Nauch. Dokl. vy̆ssh. Shk. Biol. Nauki* (112) 1973 (4) : 14–17. (In Russian.)

—— 1975. Specific features in the helminthofauna of Clupeiformes of the south seas. *Trudy̆ biol.-pochvenn. Inst., Vladivostok* (nov. ser.) **26** : 143–151. (In Russian.)

—— 1976. [*Parasitic worms in food fishes of the southern seas*], 183 pp. Kiev. (In Russian.)

—— 1978. On studies in trematodofauna of the Indian and Atlantic Oceans fishes. *Biol. Morya, Kiev* **45** : 90–99. (In Russian.)

Pelseneer, P. 1906. Trematodes parasites de mollusques marins. *Bull. scient. Fr. Belg.* **40** : 161–186.

—— 1926. La proportion relative des sexes chez les animaux et particulierement chez les molluscs. *Mém. Acad. r. Belg. Cl. Sci.* 8° (ser. 2) **8** : 258 pp.

Pigulewsky, S. W. 1938. Eine neue Trematode aus Fam. Steringophoridae. *In Livro Jubilar do Professor Lauro Travassos* : 389–390. Rio de Janeiro.

Poche, F. 1926. Das System der Platodaria. *Arch. Naturgesch.* (Abt. A) **91** : 1–459.

Polyansky, Y. I. 1955. Parasites of fish of the Barents Sea. *Trudy̆ zool. Inst. Leningr.* **19** : 5–170. (In Russian; English translation: I.P.S.T. 1966, 158 pp.).

Prevot, G. 1965. Complément à la connaissance de *Proctoeces maculatus* (Looss, 1901) Odhner, 1911 [syn. *P. erythraeus* Odhner, 1911 et *P. subtenuis* (Linton, 1907) Hanson, 1950]. (Trematoda, Digenea, Fellodistomatidae.) *Bull. Soc. zool. Fr.* **90** : 175–179

Price, E. W. 1934. New digenetic trematodes from marine fishes. *Smithson. misc. Collns* **91** (7) : 1–8.

Prudhoe, S. & Baylis, H. A. 1957. Class Trematoda. *In Plymouth Marine Fauna. Third edition* : 77–88. Plymouth.

—— **& Bray, R. A.** 1973. Digenetic trematodes from fishes. *Rep. B.A.N.Z. Antarctic Res. Exped.* **8B** : 195–225.

—— —— in press. The platyhelminth parasites of amphibians.

Rathke, J. 1799. Iagttagelser henhørende til Indvoldeormenes og Bløddyrenes Naturhistorie. *Skr. Naturh.-Selsk. Kiøbenhavn* **5** : 61–148.

Rees, G. 1953. Some parasitic worms from fishes off the coast of Iceland. II. Trematoda (Digenea). *Parasitology, Cambridge* **43** : 15–26.

—— 1970. Some helminth parasites of fishes of Bermuda and an account of the attachment organ of *Alcicornis carangis* MacCallum, 1917 (Digenea : Bucephalidae). *Parasitology, Cambridge* **60** : 195–221.

Rees, W. J. 1947. A cercaria of the genus *Haplocladus* from *Nucula nucleus* (L.). *J. mar. biol. Ass. U.K.* **26** : 602–604.

Ronald, K. 1960. The metazoan parasites of the Heterosomata of the Gulf of St. Lawrence. VI. Digenea. *Can. J. Zool.* **38** : 923–937.

Rudolphi, C. A. 1809. *Entozoorum sive vermium intestinalium historia naturalis.* Vol. 2. 457 pp. Amstelaedami.

—— 1819. *Entozoorum synopsis cui accedunt mantissa duplex et indices locupletissimi.* 811 pp. Berolini.

Scott, J. S. 1975*a*. Incidence of trematode parasites of American plaice (*Hippoglossoides platessoides*) of the Scotian shelf and Gulf of St. Lawrence in relation to fish length and food. *J. Fish. Res. Bd Can.* **32** : 479–483.

—— 1975*b*. Geographic variation in incidence of trematode parasites of American plaice (*Hippoglossoides platessoides*) in the northwest Atlantic. *J. Fish. Res. Bd Can.* **32** : 547–550.

Sey, O. 1968. Parasitic helminths occurring in Adriatic fishes. Part 1 (Flukes). *Acta adriat.* **13** (4) : 1–15.

—— 1970. Parasitic helminths occurring in Adriatic fishes. Part II (flukes and tapeworms). *Acta adriat.* **13** (6) : 1–16.

Shimazu, T. 1972. A metacercaria of the genus *Proctoeces* (Fellodistomatidae : Trematoda) from an abalone, *Haliotis discus hannai*, of Rebun Island, Hokkaido. *Bull. Jap. Soc. scient. Fish.* **38** : 813–816.

Siddiqi, A. H. & Cable, R. M. 1960. Digenetic trematodes of marine fishes of Puerto Rico. *Scient. Surv. P. Rico* **17** : 257–368.

Skrjabin, K. I. & Guschanskaja, L. K. 1956. [System of trematodes of the suborder Hemiurata (Markevitsch, 1951) Skrjabin et Guschanskaja, 1954.] *Trudy gel'mint. Lab.* **8** : 144–158. (In Russian.)

—— —— 1958. [Suborder Azygiata La Rue, 1957.] *In* K. I. Skrjabin (Ed.) [*Trematodes of animals and man. Principles of trematodology.*] **14** : 667–819. Moscow. (In Russian.)

—— **& Koval, V. P.** 1957. [Family Fellodistomatidae Nicoll, 1913.] *In* K. I. Skrjabin (Ed.) [*Trematodes of animals and man. Principles of trematodology.*] **13** : 163–452. Moscow. (In Russian.)

—— —— 1966. [Superfamily Allocreadioidea Nicoll, 1934.] *In* K. I. Skrjabin (Ed.) [*Trematodes of animals and man. Principles of trematodology.*] **22** : 177–182. Moscow. (In Russian.)

—— —— 1974. [Family Walliniidae (Yamaguti, 1958) Skrjabin and Koval, 1966.] *In* K. I. Skrjabin (Ed.) [*Trematodes of animals and man. Principles of trematodology*] **25** : 5–26. Moscow. (In Russian.)

—— *et al.* 1964. *Keys to the trematodes of animals and man.* (Translated R. W. Dooley; edited H. P. Arai.) 351 pp. Urbana.

Sogandares-Bernal, F. 1955. Some helminth parasites of fresh and brackish water fishes from Louisiana and Panama. *J. Parasit.* **41** : 587–594.

—— & **Hutton, R. F.** 1959. Studies on the helminth parasites of the coast of Florida. I. Digenetic trematodes of marine fishes from Tampa and Boca Ciega Bays with descriptions of two new species. 1. *Bull. mar. Sci. Gulf Caribb.* **9** : 53–68.

Srivastava, C. B. & Ghosh, R. K. 1968. On a new species of genus *Fellodistomum* Stafford, 1904 (Trematoda : Fellodistomidae) with redescription of *F. agnotum* Nicoll, 1909. *Indian J. Helminth.* **20** : 46–52.

Srivastava, H. D. 1935. New parasites of the genus *Orientophorus* n. gen. (Family Fellodistomidae) from an Indian fresh-water fish, *Clupea ilisha. Parasitology, Cambridge* **27** : 374–382.

—— 1937. New fellodistomids (Trematoda) from Indian food fishes. Part III – a new parasite of the genus *Haplocladus* Odhner, 1911, from the gut of an Indian marine fish. *Proc. Indian Sci. Congr.* (Hyderabad) **24** : 294–295.

—— 1939. New fellodistomids (Trematoda) from Indian hosts, Part II. Three new parasites of the subfamily Discogasteroidinae from Indian marine food-fishes. *Indian J. vet. Sci.* **9** : 91–95.

—— 1941. New fellodistomids (Trematoda) from Indian fishes. Part III. A new parasite of the genus *Haplocladus* Odhner, 1911, from an Indian marine fish. *Indian J. vet. Sci.* **11** : 42–44.

Stafford, J. 1904. Trematodes from Canadian fishes. *Zool. Anz.* **27** : 481–495.

Stossich, M. 1886. I distomi dei pesci marini e d'acqua dolce. Lavoro monografico. *Progr. Ginnasio comm. sup. Trieste* (anno 1886) : 1–66.

—— 1887. Brani di elmintologia Tergestina. *Boll. Soc. adriat. Sci. nat.* **10** : 90–96.

—— 1888. Appendice al lavoro 'I distomi dei pesci marini e d'acqua dolce.' *Progr. Ginnasio comm. sup. Trieste* (anno 35, 1887–8) : 95–105.

—— 1889. Brani di elmintologia Tergestina. *Boll. Soc. adriat. Sci. nat.* **11** : 23–30.

—— 1899. La sezione degli echinostomi. *Boll. Soc. adriat. Sci. nat.* **19** : 11–16.

Strelkov, J. A. 1960. Endoparasitic worms of marine fishes of East Kamchatka. *Trudȳ zool. Inst. Leningr.* **28** : 147–196. (In Russian.)

Stunkard, H. W. & Nigrelli, R. F. 1930. On *Distomum vibex* Linton, with special reference to its systematic position. *Biol. Bull. mar. biol. lab., Woods Hole* **58** : 336–343.

—— & **Uzmann, J. R.** 1959. The life-cycle of the digenetic trematode, *Proctoeces maculatus* (Looss, 1901) Odhner, 1911 [syn. *P. subtenuis* (Linton, 1907) Hanson, 1950], and a description of *Cercaria adranocerca* n. sp. *Biol. Bull. mar. biol. Lab., Woods Hole* **116** : 184–193.

Tauson, A. 1917. *Adolescaria ophiurae*, a parasite of *Ophiura sarsi* Lütk. *Zool. Vêst.* **2** : 149–218. (In Russian and English.)

Teixeira de Freitas, J. F. & Kohn, A. 1965. Nova espécie do genero *Tergestia* Stossich, 1899 (Trematoda, Fellodistomidae). *Mems Inst. Oswaldo Cruz* **63** : 291–297.

Thulin, J. 1973. *Protomonascus nybelini* gen. et sp. n. (Trematoda : Fellodistomidae) from *Elops senegalensis* Regan, 1909, on the west coast of Africa. *J. Parasit.* **59** : 648–649.

—— 1974. *Protomonascus nybelini* Thulin, 1973, a synonym for *Elopsium ghanense* Fischthal and Thomas, 1972. *J. Parasit.* **60** : 433.

Timon-David, J. 1934. Recherches sur les Trématodes parasites des oursins en Méditerranée. *Bull. Inst. océanogr. Monaco* (652) : 1–16.

—— 1938. On parasitic trematodes in echinoderms. *In Livro Jubilar do Professor Lauro Travassos* : 467–473. Rio de Janeiro.

Travassos, L., Teixeira de Freitas, J. F. & Bührnheim, P. F. 1965. Trematódeos de peixes do litoral capixaba: *Monascus netoi* sp. n., parasita de vento leste. *Atas Soc. Biol. Rio de J.* **9** : 46–48.

—— —— —— 1967. Relatório da excursao do Instituto Oswaldo Cruz ao Estado do Espirito Santo em novembro de 1964. *Bolm Mus. Biol. Prof. Mello-Leitão* (Zool.) **31** : 1–54.

Uzmann, J. R. 1953. *Cercaria milfordensis* nov. sp., a microcercous trematode larva from a marine bivalve, *Mytilus edulis* L., with special reference to its effect on the host. *J. Parasit.* **39** : 445–451.

Van Duzee, E. P. 1897. A preliminary review of the North American Delphacidae. *Bull. Buffalo Soc. nat. Sci.* **5** : 225–261.

Vlasenko, P. 1931. Zur Helminthofauna der Schwarzmeerfische. *Trudȳ karadah. nauch. Sta. T.I. Vyazems'koho* **4** : 88–136. (In Russian.)

Ward, H. B. 1917. On the structure and classification of North American parasitic worms. *J. Parasit.* **4** : 1–13.

White, I. C. 1972. On the ecology of an adult digenetic trematode *Proctoeces subtenuis* from a lamellibranch host *Scrobicularia plana. J. mar. biol. Ass. U.K.* **52** : 457–467.

Willemoes-Suhm, R. von 1873. *Leioderma*, new abyssal genus combining the characters of the Sipunculacea and Priapulacea. *Nature, Lond.* **8** : 28–29.

Winter, H. W. 1954. *Proctoeces macrovitellus* nov. sp., de un pez embiotocido del oceano Pacifico del norte (Tremat., Fellodistom.). *Ciencia Méx.* **14** : 140–142.

—— 1960. Algunos trematodos digeneos de peces marinos de aguas del oceano Pacifico del sur de California, U.S.A. y del litoral Mexicano. *An. Inst. Biol. Univ. Méx.* **30** : 183–208.

Woodcock, H. M. 1912. Vermidea. *Int. Cat. scient. Lit.* (1911) N. Zoology **6** : 1–52.

Yamaguti, S. 1934. Studies on the helminth fauna of Japan. Pt 2. Trematodes of fishes. I. *Jap. J. Zool.* **5** : 249–541.

—— 1938. *Studies on the helminth fauna of Japan. Part* 21. *Trematodes of fishes. IV.* 139 pp. Kyôto.

—— 1940. Studies on the helminth fauna of Japan. Part 31. Trematodes of fishes. VII. *Jap. J. Zool.* **9** : 35–108.

—— 1942. Studies on the helminth fauna of Japan. Part 39. Trematodes of fishes mainly from Naha. *Biogeographica, Tokyo* **3** : 329–397.

—— 1951. Studies on the helminth fauna of Japan. Part 44. Trematodes of fishes. IX. *Arb. Med. Fak. Okayama* **7** : 247–282.

—— 1952. Parasitic worms mainly from Celebes. Part 1. New digenetic trematodes of fishes. *Acta Med. Okayama* **8** : 146–198.

—— 1953*a*. *Systema helminthum. Part* 1. *Digenetic trematodes of fishes.* 405 pp. Tokyo.

—— 1953*b*. Parasitic worms mainly from Celebes. Part 3. Digenetic trematodes of fishes. II. *Acta Med. Okayama* **8** : 257–295.

—— 1958. *Systema helminthum. Vol.* 1. *The digenetic trematodes of vertebrates.* 1575 pp. New York.

—— 1970. *The digenetic trematodes of Hawaiian fishes.* 436 pp. Tokyo.

—— 1971. *Synopsis of digenetic trematodes of vertebrates.* Vol. 1. 1074 pp. Vol. 2. 349 pls. Tokyo.

—— 1975. *A synoptical review of life histories of digenetic trematodes of vertebrates with special reference to the morphology of their larval forms.* xxxxxxxiii + 590 pp. 219 pls. Tokyo.

—— **& Matumura, H.** 1942. Two new species of fish trematodes from Hokkaido. *Trans. Sapporo nat. Hist. Soc.* **17** : 117–122.

Yeh, L.-S. & Fotedar, D. N. 1958. A review of the trematode genus *Astiotrema* in the family Plagiorchiidae. *J. Helminth.* **32** : 17–32.

Zaidi, D. A. & Khan, D. 1977. Digenetic trematodes of fishes from Pakistan. *Bull. Dep. Zool. Univ. Panjab.* (N.S.) **9** : 1–56.

Zernov, S. A. 1913. [To the question of the study of life in the Black Sea.] *Zap. imp. Akad. Nauk* **32** : 1–299. (In Russian.)

Zhukov, E. V. 1959. [Class Cestoda: class Trematoda: class Nematoda: class Acanthocephala.] *In* A list of the fauna of the sea waters of the South Sakhalin and South Kuril Islands. *Issled. dal'nevost. Morei SSSR* **6** : 198–200.

—— 1960. Endoparasitic worms of the fishes in the Sea of Japan and South-Kuril shallow-waters. *Trudȳ zool. Inst. Leningr.* **28** : 3–146. (In Russian.)

Zschokke, F. 1896. Zur Faunistik der parasitischen Würmer von Süsswasserfischen. *Zentbl. Bakt. ParasitKde*, Abt. 1 **19** : 772–784.

Manuscript accepted for publication 14 February 1979

British Museum (Natural History)

New Publications

Invertebrate Animals Collection & Preservation

Compiled by R. J. Lincoln & J. G. Sheals

Morphology, classification and biology of all invertebrate groups, except for insects. Collecting equipment, techniques and preservatives. A comprehensive well-illustrated manual for undergraduates, research workers and operatives 'in the field'.

Co-published with Cambridge University Press. Paperback £3

British Marine Amphipoda: Gammaridea

R. J. Lincoln

Descriptions and figures of all 271 species recorded from British coasts and the adjacent continental shelf.

Hard bound £50

Parasitic Copepoda of British Fishes

Z. Kabata

Keys to, and descriptions of, all species known to parasitize fishes in British waters to time of writing. Over 2,000 illustrations. A Ray Society publication.

Hard bound £30

Titles to be published in Volume 37

Miscellanea

The echinoderms of Aldabra and their habitats. By N. A. Sloan, Ailsa M. Clark & J. D. Taylor

The anatomy, phylogeny and classification of bariliine cyprinid fishes. By G. J. Howes

The Fellodistomidae (Digenea) of fishes from the northeast Atlantic. By Rodney A. Bray & David L. Gibson

Printed by Henry Ling Ltd, Dorchester